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TESIS DOCTORAL

Multi-scale approach to forest functioning of *Pinus sylvestris* L. and *Fagus sylvatica* L. mixtures of the Pyrenees under global change

Ester González de Andrés

Pamplona-Iruñea 2018

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Multi-scale approach to forest functioning of *Pinus sylvestris* L. and *Fagus sylvatica* L. mixtures of the Pyrenees under global change

ESTER GONZÁLEZ DE ANDRÉS

Memoria presentada para optar al grado de Doctora con mención Internacional por la Universidad Pública de Navarra

Pamplona – Iruñea, Marzo de 2018

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HACEN CONSTAR:

Que el trabajo descrito en la presente memoria, titulado "**Multi-scale approach to forest functioning of *Pinus sylvestris* L. and *Fagus sylvatica* L. mixtures of the Pyrenees under global change**" que presenta Dña. Ester Gonzáles de Andrés para optar al título de Doctora con mención de "Doctora Internacional", ha sido desarrollado bajo su dirección en el Área de Ecología del Departamento de Ciencias del Medio Natural de la Universidad Pública de Navarra y reúne todos los requisitos necesarios para su defensa.

Pamplona – Iruñea, Mayo de 2018

Fdo: Juan A. Blanco Vaca

Fdo: J. Bosco Imbert Rodríguez

Results obtained in this study have been presented in the following publications and in the following conferences:

González de Andrés, E., Camarero, J.J., Blanco, J.A., Imbert, J.B., Lo, Y., Sangüesa-Barreda, G. & Castillo, F.J. (2018) Tree-to-tree competition in mixed European beech – Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions. *Journal of Ecology*, 00: 1-17. DOI: 10.1111/1365-2745.12813

González de Andrés, E., Seely, B., Blanco, J.A., Imbert, J.B., Lo, Y. & Castillo, F.J. (2017) Increased complementarity in water-limited environments in Scots pine and European beech mixtures under climate change. *Ecohydrology*, 10: e1810. DOI: 10.1002/eco.1810

González de Andrés, E., Camarero, J.J., Blanco, J.A., Imbert, J.B., Lo, Y., Sangüesa-Barreda, G. & Castillo, F.J. (2017) Increasing droughts and tree density reduces European beech response to rising atmospheric CO_2 concentration. *IUFRO 125th Anniversary Congress*, Friburg, Germany, September 19-22.

González de Andrés E., Blanco J.A., Seely B., Imbert J.B., Lo Y. & Castillo F.J. (2015) Site fertility is more important than climate to produce overyielding in mixed Scots pine-European beech stands. *IV International Conference Forest and Water in a Changing Environment*, Kelowna, Canada, July 6-9.

González de Andrés E., Camarero J.J., Blanco J.A., Imbert J.B., Lo Y.H., Sangüesa-Barreda G. & Castillo F.J. (2016) Growth and carbon isotopes relationships in Pinus sylvetris (L.) and Fagus sylvatica (L.) mixedwoods in the SW Pyrenees. *EuMIXFOR Final Conference: Integrating Scientific Knowledge in Mixed Forests*, Prague, Czech Republic, September 5-7.

González de Andrés E., Seely B., Blanco J.A., Imbert J.B., Lo Y.H. & Castillo F.J. (2016) Scots pine and European beech mixtures as an adaptation strategy in the face of climate change in drought-prone sites in the SW Pyrenees. *EcoSummit 2016. Ecological Sustainability: Engineering Change*, Montpellier, France, August 29-September 1.

González de Andrés E., Blanco J.A., Imbert J.B. & Castillo F.J. (2014) Scots pine growth is favoured in mixed pine-beech stands in low fertility sites. *5th International Conference on Mediterranean Pines (Medpine5)*, Solsona, Spain, September 22-26.

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ABBREVIATIONS

A	Rate of photosynthesis
a	Diffusion fractionation across the boundary layer and the stomata
AIC	Akaike's information criterion
AICc	Akaike's information criterion corrected for small sample size
b	Rubisco enzymatic biologic fractionation
BAI	Basal area increment
C_a	Atmospheric CO_2 concentration
$CanT_{Actual}$	Soil-limited actual transpiration
$CanT_{Demand}$	Energy-limited transpiration demand
C_i	Intercellular CO_2 concentration
CONT	Continental site
CRU	Climate Research Unit
dbh	Diameter at breast height (1.3 m)
DCI	Distance-dependent competition index
EEMD	Ensemble empirical mode decomposition
EMD	Empirical mode decomposition
ENSO	El Niño-Southern Oscillation
FORECAST	Forest and Environmental Change Assessment Tool
ForWaDy	Forest Water Dynamics
g	Stomatal conductance
GCD	Global change driver
GCM	Global Circulation Model
GRH	Growth rate hypothesis
IMF	Intrinsic mode function
iWUE	Intrinsic water-use efficiency
LMM	Linear mixed effects model
MED	Mediterranean site
MT-CLIM	MounTain microCLIMate simulation model
NAO	North Atlantic Oscillation
NPP	Net primary production
NUE	Nitrogen-use efficiency
OC	Oscillatory component

PC	Principal component
PCA	Principal component analysis
PDO	Pacific Decadal Oscillation
PET	Potential evapotranspiration
PNL	Progessive N limitation hypothesis
P-PET	Water balance
R^2	Coefficent of determination
R^2c	Conditional coefficient of determination
R^2m	Marginal coefficent of determination
RCP	Representative concentration pathway
RDA	Redundacy analysis
SGH	Stress Gradient Hypothesis
SLP	Sea level pressure
$Sp_{i,j}$	Species i proportion at year j
SPEI	Standarized Precipitation Evapotranspiration Index
SST	Sea surface temperature
TDI	Transpiration deficit index
TRW	Tree-ring width
VIF	Variance inflation factor
WUE	Water-use efficiency
$Y_{mixed\ i,j}$	Stemwood yield of species i year j growing in a mixed stand
$Y_{mono\ i,j}$	Stemwood yield of species i at year j growing in a pure stand
$\delta^{13}C$	Composition of stable C isotopes

SUMMARY

Nowadays, mixed-species forests are increasingly recognized as superior to pure stands regarding the provision of a full range of ecosystem goods and services. The management of forests in a mixed condition is considered as an adaptation strategy in the face of global change because of their greater stability to predicted increasing uncertainty in environmental conditions. Further, mixed forests can be more productive than pure stands. However, there are still important knowledge gaps about the impact of changes in resources availability on mixing effects and forest processes, such as water use, tree growth and nutrient cycling.

Mixed forests of Scots pine and European beech are widespread across Europe and reach their southwestern distribution limit in the Pyrenees. This region is likely to be highly sensitive to climate change so the study of these rear-edge forests can provide valuable insights towards understanding long-term impacts of warmer and/or drier conditions that can develop earlier than in core distribution areas. This research thesis aims to assess natural ecological succession within Scots pine – European beech mixed stands located in the Pyrenean region of Navarre (northern Spain) and to contribute to a better understanding of responses of the functioning of such mixtures to global change drivers using a multi-scale approach. In order to do this, a set of unmanaged experimental plots were established in two forest stands of contrasting climatic and fertility characteristics: a sub-xeric site located at low elevation with a cool and dry Mediterranean climate and high productivity (Aspurz), and a mesic site situated at high elevation characterized by cold-wet continental climate and low productivity (Garde).

Firstly, intrinsic water-use efficiency (iWUE) and secondary growth chronologies of both Scots pine and European beech were reconstructed at tree-level for the period 1980-2013 using width and stable carbon isotope composition information from tree rings. We assessed the influence of climate and atmospheric CO_2 concentration on growth and iWUE in relation to intra- and interspecific competition, which was estimated by means of a distance-dependent competition index. On one hand, we found complementarity effects on Scots pine only at the continental site likely due to light-related interactions with European beech trees. However, at the drought-prone Mediterranean site strong competition for water with beech may override light-related mixing effects on Scots pine growing in mixtures, as is highlighted by the increase of iWUE of pines subjected to high interspecific competition. On the other hand, the reduction of iWUE of European beech as interspecific competition increases suggests a water stress release when pine is admixed. Both species show contrasting growth – iWUE relationships. Negative growth response of Scots pine to increasing iWUE may be related to a combination of water and nutrient limitations. Although this association was positive for European beech, we found a progressive uncoupling of growth, iWUE and rising atmospheric CO_2 concentration during the 20th century.

Secondly, the process-based, ecosystem-level FORECAST Climate model was calibrated for the two study sites in order to explore mixing effects on Scots pine – European beech mixtures at longer time scales and to assess possible consequences of predicted climate change. The stand-level simulations support the results from the dendrochronological approach, although slight differences between both approaches were reported due to methodological issues. Growing in mixtures with

European beech, Scots pine trees were predicted to have larger crowns with higher N contents as a result of improved nutrient supply due to the higher quality beech leaf litter, which enhanced light absorption and translated into increased pine growth. Climate change simulations predicted increases of biomass accumulation at the cold-wet continental site (+ 11 %) and reductions at the sub-xeric Mediterranean site (- 33 %), so endorsing the hypothesis of light-related benefits cancelled out by competition for water when this resource becomes more limiting. Regarding European beech, the predicted reduction in canopy transpiration and the consequent complementarity when Scots pine is admixed, especially under climate change scenarios, uphold the water-related nature of mixing effects. Overall, the results from both approaches agree with the "complementarity- competition" framework. The contrasting nature of mixing effects on both species could explain growth reductions of Scots pine and neutral or positive responses of European beech growth as water exerts a great limitation in the study region, particularly at the Mediterranean site, and this limitation is expected to increase. The results emphasize the importance of considering functional traits involved in a given mixture and site-specific factors rather than only species diversity.

Finally, a 16-year series of production, nutrient concentration and N:P:K stoichiometry of leaf litter were collected during autumn months at both study sites. Such series were split into oscillatory components and trends following the ensemble empirical mode decomposition (EEMD) method in order to evaluate the climatic influence. The connection with other forest processes was also assessed based on the close linkage between litterfall dynamics and nutrient return to soils and thus forest productivity. Leaf litter series reflected the gradual succession towards mixed forests during the last decades, which is more advanced at the Mediterranean site, and underscored the consequences for forest nutrient cycles due to the higher nutrient concentration in beech litter. Large-scale atmospheric-oceanic circulation patterns (NAO, ENSO and PDO), through their influence of water availability in the Pyrenees, accounted for similar or even higher variation of leaf litter dynamics than locally-measured climatic variables. The strong impact of water availability on leaf litter seasonality and composition shows the complex interactions between water and nutrient limitations. Trends in stoichiometry of leaf litter suggest an increasing P limitation of decomposition particularly at the Mediterranean site, with the consequent decrease in nutrient release, in Pyrenean Scots pine – European beech mixtures largely related to rising atmospheric N deposition. Furthermore, secondary growth of Scots pine negatively responded to increasing N:P ratios of litter fallen 3 years prior, while the connection between N:K ratio and pine iWUE highlights the important role of K in the regulation of tree water balance.

Our results emphasize the complex interconnections among water and nutrient limitations. The negative direct impact of drought on tree growth may be worsened if decreases in nutrient supply reduce capacity of trees to use water efficiently. This research proposes that Scots pine could benefit from light-related interactions with European beech, although growth reductions of pine trees growing in mixed forests might be expected due to the combined effect of water and nutrient limitation if water stress continues to rise. Our results suggest a beneficial effect of pine admixture on European beech, especially under climate change scenarios. It follows from the above, management plans focused on adapting mixed-species forests to the effects of global change need to consider the

simultaneous limitation by different resources, as well as historical land uses and site-specific factors, and their impact on intra- and interspecific interactions of a given species combination.

RESUMEN

Hoy en día, los bosques mixtos son cada vez más reconocidos como superiores a los bosques puros en cuanto a la provisión de una completa gama de bienes y servicios ecosistémicos. La gestión de los bosques en una condición mixta se considera como una estrategia de adaptación ante el cambio global debido a su mayor estabilidad ante la incertidumbre creciente que se pronostica en las condiciones ambientales. Además, los bosques mixtos pueden ser más productivos que los rodales puros. Sin embargo, todavía existen importantes vacíos de conocimiento sobre el impacto de los cambios en la disponibilidad de recursos en las interacciones entre especies y otros procesos forestales, como el uso del agua, el crecimiento de los árboles y el ciclo de nutrientes.

Los bosques mixtos de pino silvestre y haya se extienden a lo largo de Europa y alcanzan su límite de distribución suroccidental en los Pirineos. Es probable que esta región sea muy sensible al cambio climático, por lo que el estudio de estos bosques marginales puede proporcionar información valiosa para comprender los impactos a largo plazo de las condiciones más cálidas y / o más secas que pueden desarrollarse en los Pirineos antes que en las áreas centrales de su distribución. Esta tesis doctoral tiene como objetivo evaluar la sucesión ecológica natural hacia bosques mixtos de pino silvestre y haya ubicados en la región pirenaica de Navarra (norte de España) y contribuir a una mejor comprensión de las respuestas del funcionamiento de estos bosques mixtos a los efectos del cambio global utilizando un enfoque a múltiples escalas. Se estableció un conjunto de parcelas experimentales sin gestión forestal en dos bosques con distintas características climáticas y de fertilidad: un sitio sub-xérico ubicado a baja elevación con un clima mediterráneo frío y seco y alta productividad (Aspurz), y un sitio mésico situado a gran altitud caracterizado por clima continental húmedo y frío y baja productividad (Garde).

En primer lugar, a partir del estudio de los anillos de crecimiento se reconstruyeron cronologías de eficiencia intrínseca del uso del agua (iWUE) y crecimiento secundario para ambos pino silvestre y haya a escala de árbol para el período 1980-2013. Evaluamos la influencia del clima y la concentración atmosférica de CO_2 sobre el crecimiento y la iWUE en relación con la competencia intra- e interespecífica, que se estimó mediante un índice de competencia espacial. Por un lado, encontramos efectos de complementariedad en el pino solo en el sitio continental probablemente debido a las interacciones con el haya relacionadas con la luz. Sin embargo, en el sitio mediterráneo propenso a la sequía, la fuerte competencia por el agua con el haya pudo anular el efecto beneficioso de la interacción en la absorción de luz para el pino, como destaca el aumento observado de la iWUE de pinos sometidos a alta competencia interespecífica. Por otro lado, la reducción de la iWUE del haya a medida que aumenta la competencia interespecífica sugiere una reducción del estrés hídrico que sufre esta especie cuando se mezcla con pino. Ambas especies muestran una relación crecimiento – iWUE opuesta. La respuesta negativa del crecimiento del pino al aumento de la iWUE puede estar relacionada con una combinación de limitaciones por agua y nutrientes. Aunque esta relación fue positiva para el haya, también encontramos un progresivo desacoplamiento entre crecimiento, iWUE y aumento de la concentración atmosférica de CO_2 a lo largo del siglo XX.

En segundo lugar, se calibró el modelo forestal basado en procesos a nivel de ecosistema FORECAST Climate para los dos sitios de estudio con el fin de explorar los efectos de las interacciones en bosques mixtos de pino silvestre y haya a escalas temporales más largas y para evaluar las posibles consecuencias del cambio climático. Las simulaciones a nivel de rodal apoyan los resultados del análisis dendrocronológico, aunque encontramos pequeñas diferencias entre ambos enfoques debido a cuestiones metodológicas. Se predijo que cuando crecen en rodales mixtos con haya, los pinos desarrollan copas más grandes con mayor contenido en N. Esto se debe a un mejor suministro de nutrientes debido a la mayor calidad de la hojarasca del haya, lo que mejora la absorción de luz y se traduce en un mayor crecimiento del pino. Las simulaciones de cambio climático predijeron aumentos de la acumulación de biomasa en el sitio continental húmedo (+ 11%) y reducciones en el sitio mediterráneo sub-xérico (- 33%), respaldando la hipótesis de que los beneficios relacionados con la luz quedan anulados por la competencia por agua cuando este recurso se vuelve más limitante. Con respecto al haya, la reducción prevista en la transpiración del dosel y la consecuente complementariedad cuando se mezcla con pino, especialmente bajo escenarios de cambio climático, apoyan que el efecto de las interacciones interespecíficas sobre el haya está relacionado con el agua. En general, los resultados de ambos enfoques coinciden con el marco de "complementariedad-competencia". La diferente naturaleza de los efectos de las interacciones en ambas especies podría explicar las reducciones de crecimiento del pino y las respuestas neutrales o positivas del crecimiento del haya, ya que el agua ejerce una gran limitación en la región de estudio, particularmente en el sitio mediterráneo, y se espera que esta limitación aumente. Nuestros resultados enfatizan la importancia de considerar los rasgos funcionales involucrados en una determinada mezcla y los factores específicos del sitio en lugar de solo la diversidad de especies.

Finalmente, se recolectaron muestras de producción, concentración de nutrientes y estequiometría N:P:K de hojarasca durante los meses de otoño a lo largo de 16 años en ambos sitios de estudio. Estas series temporales se descompusieron en componentes oscilatorios y tendencias siguiendo el método de *ensemble empirical mode decomposition* (EEMD) para evaluar la influencia climática. También evaluamos la conexión con otros procesos forestales teniendo en cuenta la estrecha vinculación entre la dinámica de la hojarasca y el retorno de nutrientes a los suelos y, por lo tanto, la productividad forestal. La series de hojarasca reflejaron el proceso de sucesión gradual hacia los bosques mixtos durante las últimas décadas, que se encuentra más avanzada en el sitio mediterráneo, y subrayaron las consecuencias para los ciclos de nutrientes de estos bosques debido a la mayor concentración de nutrientes en la hojarasca de haya. Los patrones a gran escala de circulación atmosférica-oceánica (NAO, ENSO y PDO), a través de su influencia de la disponibilidad de agua en los Pirineos, explicaron la variabilidad de las dinámicas de la hojarasca similar o incluso mayor que las variables climáticas medidas localmente. El fuerte impacto de la disponibilidad de agua en la estacionalidad y composición de la hojarasca muestra las complejas interacciones entre las limitaciones de agua y nutrientes. Las tendencias en la estequiometría de la hojarasca sugieren un aumento en la limitación por P de la descomposición especialmente en el sitio mediterráneo, con el consiguiente descenso en la liberación de nutrientes, en bosques mixtos de pino y haya de los Pirineos en gran parte relacionada con el aumento de la deposición atmosférica de N. Además, el crecimiento secundario del pino mostró una respuesta negativa a aumentos en el ratio N:P de la hojarasca caída 3

años antes, , mientras que la conexión entre el ratio n:K y la iWUE pone de relieve el importante papel del K en la regulación del balance hídrico de los árboles.

Nuestros resultados enfatizan las complejas interconexiones entre las limitaciones de agua y nutrientes. El impacto negativo directo de la sequía en el crecimiento de los árboles puede empeorar si la disminución en el suministro de nutrientes reduce la capacidad de los árboles para usar el agua de manera eficiente. Esta investigación propone que el pino silvestre podría beneficiarse de las interacciones relacionadas con la luz con el haya, aunque podrían sufrir reducciones de su crecimiento en bosques mixtos con haya debido al efecto combinado de las limitaciones por agua y nutrientes si el estrés hídrico continúa en aumento. Nuestros resultados sugieren un efecto beneficioso de la mezcla con pino para el haya, especialmente en escenarios de cambio climático. Por lo tanto, los planes de gestión forestal enfocados en adaptar los bosques mixtos a los efectos del cambio global necesitan considerar la limitación simultánea por diferentes recursos, así como los usos históricos de la tierra y los factores específicos del sitio así como su impacto en las interacciones interespecíficas de una combinación de especies determinada.

CONTENTS

CHAPTER 2

Increased complementarity in water-limited environments in Scots pine and European beech mixtures under climate change

CHAPTER 3

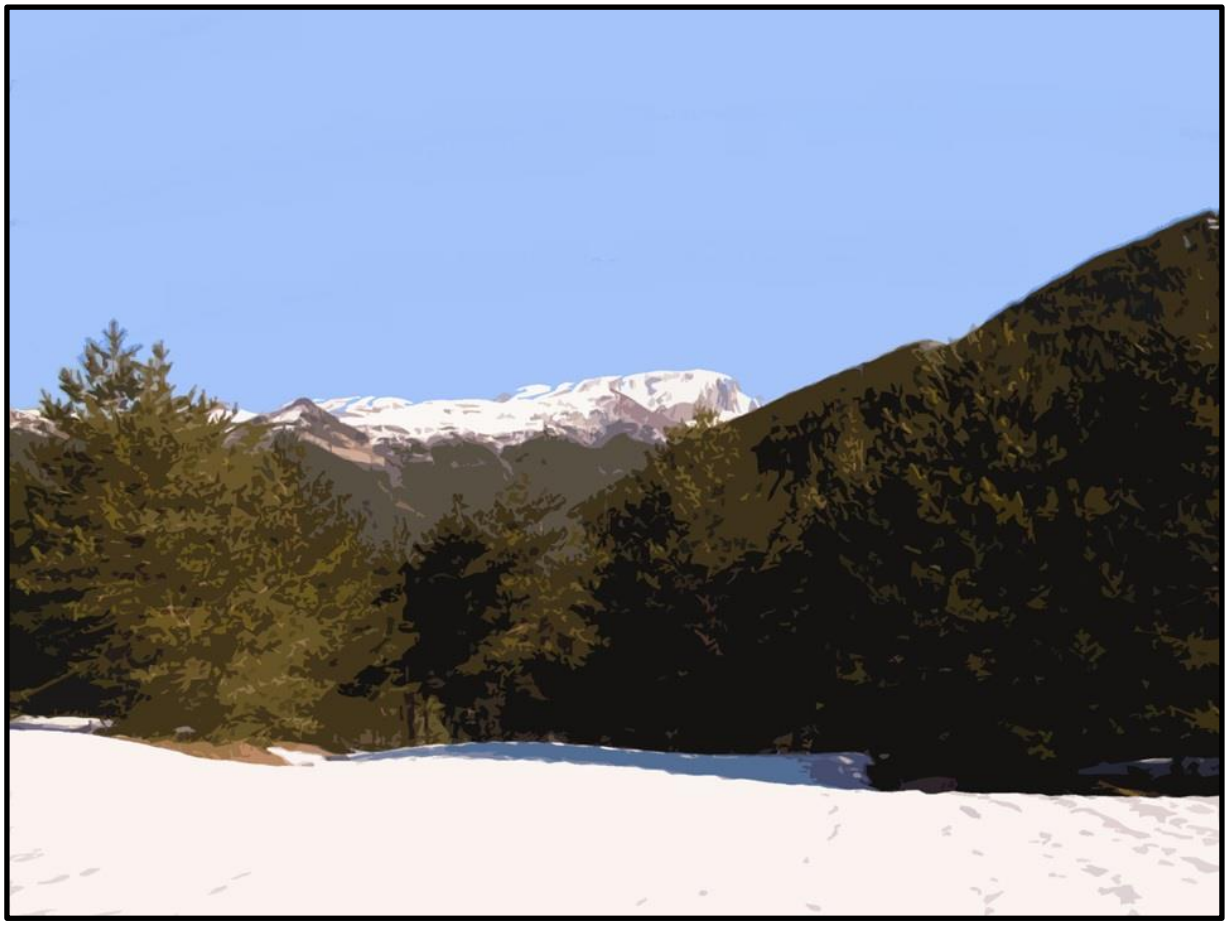
Long-term leaf litter dynamics and N:P:K stoichiometry of Scots pine and European beech mixtures are connected with large-scale circulation patterns and secondary growth

GENERAL DISCUSSION

APPENDIX A (Chapter 1)

APPENDIX B (Chapter 2)

GENERAL INTRODUCTION



1. GLOBAL CHANGE AND FORESTS

World-wide, forests cover 4.03 billion hectares, ca 30 % of Earth's total land area. They account for 75% of terrestrial gross primary production, 80% of Earth's total plant biomass and contain more carbon in biomass and soils than is stored in the atmosphere (FAO 2016). Globally, they support over half of all described species and provide a range of valuable goods and ecosystem services, including food, fiber, timber, medicine, clean water, aesthetic and spiritual values. Forests play a particularly significant role in climate regulation, owing to their low albedo and high rates of evapotranspiration (Pan et al. 2013, Anderson-Teixeira et al. 2015). Forest systems are associated with the regulation of 57% of total water runoff and about 4.6 billion people depend for all or some of their water on supplies from forest systems (Ellison et al. 2017).

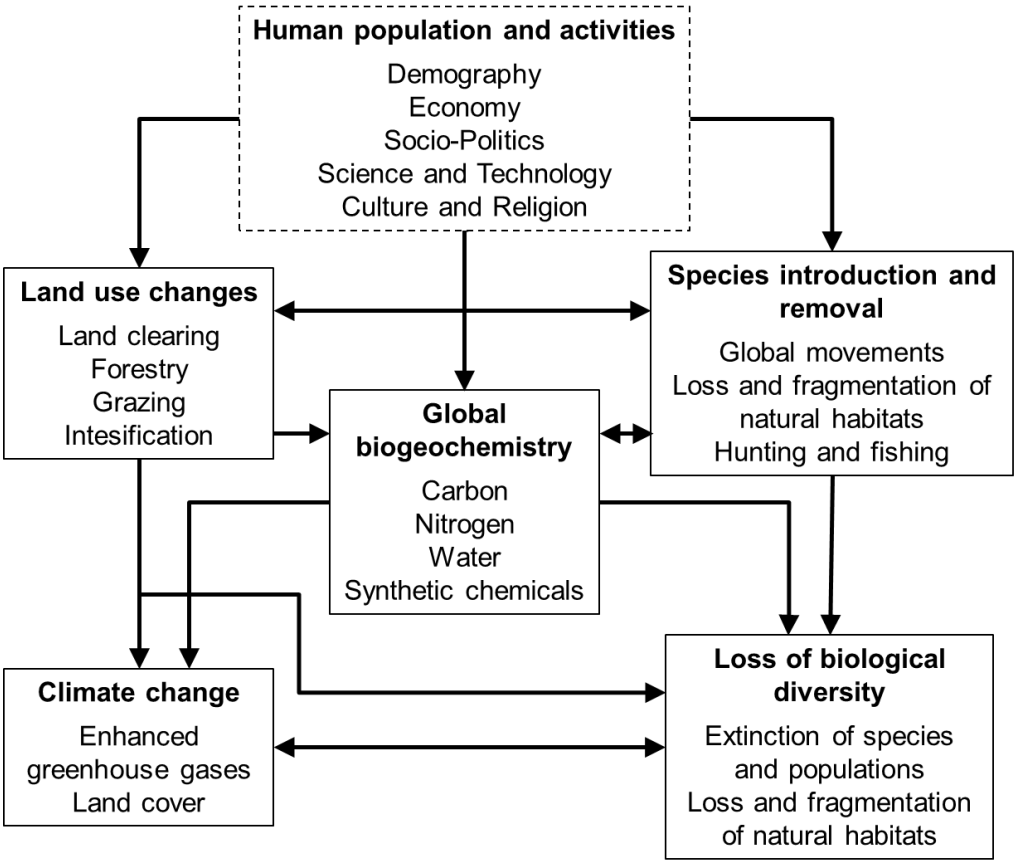


Figure 1. The components of global change and their interactions. Solid line boxes represent direct drivers and dash line boxed indirect drivers (modified from Vituosek et al. 1997).

Human appropriation of land and water for agriculture and other purposes; emission of extraneous compounds to the atmosphere and water, extraction of food, fuel, and fiber from natural ecosystems; and transport of species around the globe have pervasively influenced Earth's climate, hydrology, biogeochemistry, land cover, and species diversity (Vitousek et al. 1997, Rockström et al. 2009). The Earth and its ecosystems are undergoing rapid global change driven by natural and human-induced factors (i.e. global change drivers, GCD) that is expected to influence plant species' dominance

and distribution, primary productivity and nutrient cycles worldwide (Sala et al. 2000, Ellison et al. 2017). Demographic, economic, socio-political, cultural, scientific and technological factors (i.e. indirect drivers) cause physical and biological changes (i.e. direct drivers) on ecosystems (Fig. 1). Global change involves the simultaneous and rapid alteration of several key environmental parameters that control the dynamics of forests (Aber et al. 2001, Elser et al. 2010). Hence, forest ecosystems are currently facing unprecedented shifts in environmental conditions, with implications for biodiversity patterns, ecosystem functions and services (Anderson-Teixeira et al. 2015, Millar & Stephenson 2015).

1.1. Global change drivers

The post-industrial planet has experienced a striking increase in atmospheric concentrations of the greenhouse gases carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), which have substantially exceeded the highest concentrations recorded in ice cores during the past 800,000 years. In 2014, atmospheric CO_2 concentration (C_a) surpassed the threshold of 400 p.p.m. and this concentration may double in the 21st century relative to that previous to 1850 (IPCC 2013). From 1750 to 2011, anthropogenic CO_2 emissions have released 555 GtC and are mainly attributed to fossil fuel combustion, cement production and land use changes such as deforestation (Fig. 2A) (Nelson et al. 2006). The steep rise in C_a and other greenhouse gases has been associated with ocean acidification and alteration of global climatic regimes. Mean global surface temperature has raised an average of 0.74 ºC since the late 19th century and this warming has been particularly marked since the 1970s (Fig. 2B). Besides, air temperatures are projected to continue increasing globally, possibly by as much as 4 ºC by 2100 (IPCC 2013).

On the other hand, modification of the global hydrological cycle has been spatially heterogeneous, with precipitation increases in mid- and high-latitude land areas of the Northern hemisphere, while for other latitudinal zones precipitation trends have been less consistent (Zhang et al. 2007). Occurrence of extreme weather and climatic events has also increased since the middle of the 20th century, such as increases in either the frequency or intensity of heavy precipitation in North America and Europe, or drought events in the Mediterranean and West Africa (Trenberth 2011, IPCC 2013). Precipitation patterns are predicted to undergo further changes, with most arid and semiarid areas becoming drier and with an increase in heavy precipitation events, leading to an increased incidence in floods and droughts (IPCC 2013). Furthermore, there is evidence that main large-scale atmospheric-oceanic circulation patterns, such as the North Atlantic Oscillation (NAO), which affects the severity of winter temperatures and precipitation in Europe and eastern North America, and the El Niño – Southern Oscillation (ENSO), which has large regional effects around the world, are behaving in unusual ways that appear to be linked to global warming (Hoerling et al. 2001). Current predictions state that due to changes in moisture availability ENSO-induced rainfall variability on regional scales will intensify, while NAO is likely to become slightly more positive due to increases in greenhouse gases (Christensen et al. 2013).

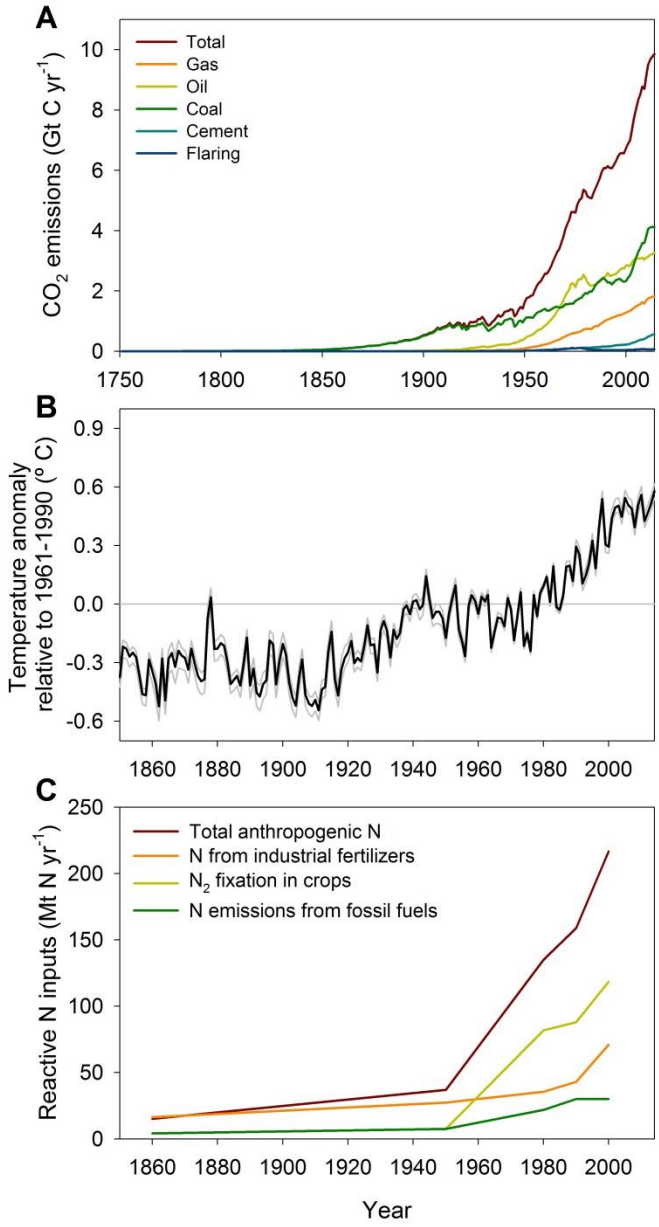


Figure 2. (A) Fossil fuel and cement CO_2 emissions by category, estimated by the Carbon Dioxide Information Analysis Center (CDIAC) based on UN energy statistics for fossil fuel combustion and US Geological Survey for cement production (Boden et al., 2011). (B) Global average land-sea temperature anomaly relative to the 1961-1990 average temperature; grey lines represent upper and lower 95 % confidence intervals (Morice et al. 2012). (C) Anthropogenic reactive nitrogen inputs to the biosphere by sources (Peñuelas et al. 2013).

Despite the growing concern for climate change impacts, global change is not restricted to climate since other drivers exert dramatic pressures on the ecosystems (Sala et al. 2000). Burning of fossil fuels, fertilizer inputs, and human-induced biological fixation of atmospheric N_2 by cultivated leguminous crops and rice have resulted in the alteration of the N biogeochemical cycle. As a consequence, concentrations of the greenhouse gas N_2O have globally increased. Likewise, fluxes of reactive N gases to the atmosphere, which afterwards are deposited downwind, have tripled since

1860 and is expected to further increase in coming decades (Fig. 2C) (Vitousek et al. 1997, Galloway et al. 2004). Long-term N loading has also been shown to alter soil nutrient cycling and promote soil acidification and leaching of nitrate and soil cations (Aber et al. 1991, Magill et al. 1997). N deposition mostly impacts northern ecosystems, especially around densely populated areas, but will likely extend to the tropics during 21st century (Galloway et al. 2004, Wei et al. 2012). Annual anthropogenic N deposition amounts to roughly 165-259 Mton N $year^{-1}$, and only ca. 22 % of these inputs ends up accumulating in the soil and biomass (Peñuelas et al. 2012). Land use changes, habitat fragmentation and biological invasions are also considered main drivers of global change and an important threat to biodiversity (Young et al. 1996, Vitousek et al. 1997).

The complex interactions among atmosphere dynamics alterations, climate change, management native communities and introduced species make it extremely difficult to forecast ecosystem changes (Dale et al. 2001), which can have both short-term or ecological and long-term or evolutionary consequences (Nelson et al. 2006). In addition, the interactions among different GCDs frequently generate non-additive effects on ecosystems that cannot be predicted based on single-factor studies (Lloyd 1999, Sala et al. 2000, Jactel et al. 2017, Lim et al. 2017, Sardans et al. 2017). The following sections summarize the combined effect of C and N altered cycles and the consequent climate change at three levels of forest ecosystems' organization: i) tree physiology and growth, ii) tree-to-tree interactions, and iii) nutrient cycles.

1.2. Impacts of global change on forest ecosystems

1.2.1. Tree physiology and growth

Despite significant rises in C_a, current levels do not suffice to saturate photosynthesis of unstressed C3 tree species (Ainsworth & Long 2005). Thus, increasing C_a will enhance the rate of carboxylation by the photosynthetic enzyme system and reduce photorespiration (Norby et al. 1999). Increased C_a might also induce a partial closure of stomata, reducing water loss by transpiration, which results in an increase in the ratio of the carbon gain to water loss, i.e. water-use efficiency (WUE) (Fig. 3A) (Farquhar et al. 1989, Körner 2000, Huang et al. 2007). This CO_2-induced improvement in primary productivity and WUE is commonly referred as fertilization effect and an enhancement of growth is expected to occur. Many tree-ring studies have reported either positive (e.g. LaMarche et al. 1984, Soulé & Knapp 2006, Martínez-Vilalta et al. 2008), or neutral to negative (e.g. Peñuelas et al. 2008, 2011, Linares & Camarero 2012, Silva & Anand 2013, Granda et al. 2014, Camarero et al. 2015) growth responses to rising C_a, what reveals the existence of other factors that influence tree responses (Aber et al. 2001).

On one hand, long-term elevated C_a exposure studies suggest that a reduction of photosynthetic capacity occurs over time (Ainsworth et al. 2004, Huang et al. 2007). Down-regulation has been associated with several processes such as a reduction of the capacity of dark reactions to process CO_2 due to decreases of leaf N concentration (Aranjuelo et al. 2005), or long-term anatomical and physiological adaptations for adjusting intercellular CO_2 concentration to rising C_a including changes in stomatal density (Ward et al. 2005). On the other hand, when trees are exposed to increased C_a,

other factors may become more important, thus limiting their ability to increase growth rates (Norby et al. 1999, Gedalof & Berg 2010, Silva et al. 2010).

Nutrient limitation is hypothesized as primary cause for reduced or lack of CO_2 fertilization effect (Luo et al. 2004, Norby et al. 2010). As a most critical component of many important structural, genetic and metabolic compounds in plant cell, N is required in relatively large quantities in connection with all growth processes (Huang et al. 2007). Trees growing under rising C_a will increase the N demand and enhance N sequestration in long-lived biomass and soils, thus N availability will progressively decline (Reich et al. 2006). As a consequence, long-term tree growth responses to increased C_a could be reduced due to the N limitation, as predicted by the progressive N limitation (PNL) hypothesis (Luo et al. 2004). Furthermore, reduction of tissue N concentrations and increase of non-structural carbohydrates and secondary metabolites can alter tree resistance to pests and herbivores (Aber et al. 2001). The PNL hypothesis would be particularly important in temperate and boreal forests, whose young soils have been traditionally considered as N-limited (Aerts & Chapin 2000, Vitousek et al. 2010). The synergistic effect of increased C_a and rising N deposition is expected to stimulate forest productivity (Townsend et al. 1996), through increases in photosynthetic rates and/or leaf area and thus light interception (Lim et al. 2015). In fact, increases in forest growth in response to N deposition have been reported in some boreal and temperate forests (e.g. Hyvönen et al. 2008, Thomas et al. 2010, Pretzsch et al. 2014). However, atmospheric N deposition affects forest ecosystems in a complex way. Results from long-term N-fertilization experiments suggests that the growth enhancement observed after N addition emerges mainly from changes in C allocation from fine roots and mycorrhizal fungi to woody components rather than increasing photosynthesis (Lim et al. 2015). Furthermore, several studies report neutral or negative growth responses despite the increase in C_a and N deposition (e.g. Peñuelas et al. 2011, de Vries et al. 2014), and even tree mortality under N saturation (Magill et al. 2004). Recently, de Vries et al. (2014) from a synthesis of N addition experiments pointed out that high N deposition rates produce a declining response in forest productivity. All together, these results emphasise that other factors override the potential growth benefits, such as other nutrients or water availability.

Even though N limitation is widespread in forest ecosystems, co-limitation of N and phosphorus (P), or P limitation only frequently occur especially in tropical forests where soils are older and highly leached (Aerts & Chapin 2000, Vitousek et al. 2010, Harpole et al. 2011) and in Mediterranean areas due to the interaction with water availability (Sardans & Peñuelas 2004, Sardans et al. 2006). Increases in P-limitation and foliar N:P ratios have been reported in different forest ecosystems due to nutrient imbalances related with increased N deposition (Braun et al. 2010, Sardans et al. 2011, Jonard et al. 2015, Talkner et al. 2015). P plays a key role in many plant processes such as energy metabolism, synthesis of nucleic acids and membranes, photosynthesis, respiration, nitrogen fixation and enzyme regulation (Raghothama 1999). In addition, P availability has a positive effect on WUE (Sardans & Peñuelas 2007) Therefore, P deficiency leads to reduced tree growth.

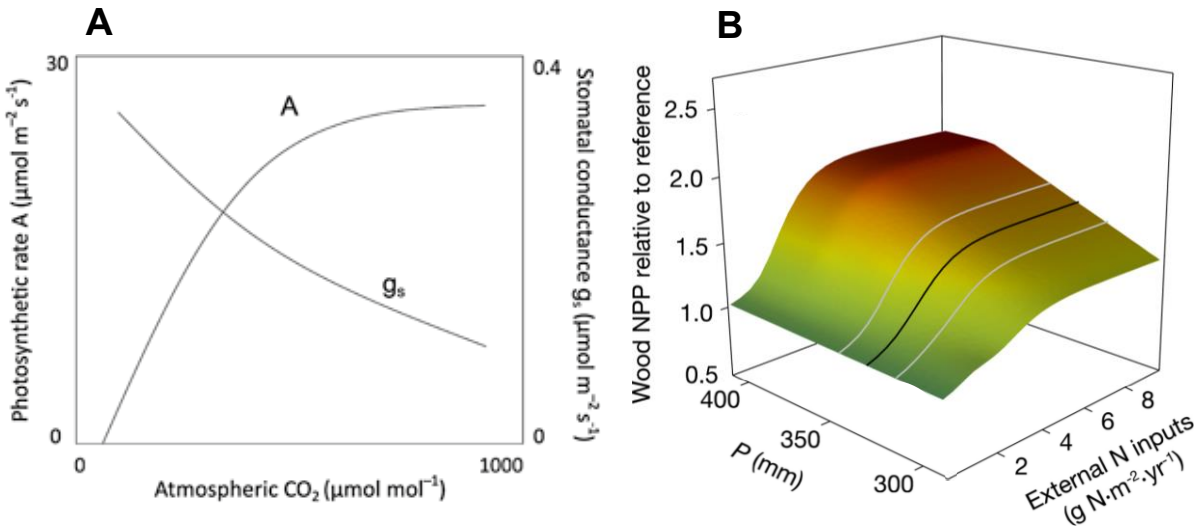


Figure 3. (A) Relationship between photosynthetic rate (A), stomatal conductance for CO_2 (g_s) and atmospheric CO_2 concentration (C_a) from unstressed *Populus deltoides* trees (from Silva & Anand 2013). (B) Net primary productivity (NPP) of woody mass relative to reference null N inputs in response to a combination between external N inputs and growing season precipitation of *Pinus sylvestris* L. (from Lim et al. 2017).

In addition to nutrients and pollutants, climate also interacts with C_a regulating the water balance and growth of trees. Despite the rising C_a, which leds to increases in WUE (Waterhouse et al. 2004, Huang et al. 2007), no clear evidence of positive tree growth response has been found in the last decades (Peñuelas et al. 2011, Silva & Anand 2013). Indeed, global growth response patterns in relation to temporal changes in WUE have been shown to be latitude-dependent (Silva & Anand 2013). In cold regions, where water availability is usually not a limiting factor, the synergistic effect of warming and elevated C_a stimulate tree growth, as it has been observed in boreal and temperate forests located at latitudes greater than 40º N (Silva et al. 2010). However, the growth-WUE relationship becomes progressively more negative in Mediterranean, arid, subtropical and tropical forests (e.g. Peñuelas et al. 2008, Nock et al. 2010, Linares & Camarero 2012, Levesque et al. 2014, Camarero et al. 2015). In warm regions, higher temperatures often lead to increased leaf to air vapour pressure deficit, with the subsequent reduction of stomatal conductance and the enhancement of WUE (Wullschleger et al. 2002, Waterhouse et al. 2004), at the expense of lower photosynthetic rate (Lloyd & Farquhar 2008). Hence, water stress could cancel out the CO_2 fertilizer effect and the beneficial influence of enhanced WUE in terms of secondary growth unless water availability is enough to maintain foliage and fine roots (i.e. high priority organs) (Levesque et al. 2014). It is noteworthy that the afore-mentioned global patterns may be modified by regional and local trends affected by site-specific factors such as altitude, slope, nutrients availability, and so on.

Finally, multiple interactions among the C_a, N deposition and climate over the physiological and growth response of trees may occur. Interactions among different drivers introduce further complexity, because their effects can be synergistic or antagonistic, and not simply additive (Dieleman et al. 2012, Sardans et al. 2017). Understanding the dependencies among GCDs is highly relevant in order to develop proper models that predict structure and functioning alterations, including C storing

capacity, of forest ecosystems in the face of global change (Peñuelas et al. 2013, Jonard et al. 2015). However, such observational or experimental studies in forests are still scarce (but see Dziedek et al. 2016, Lim et al. 2017). Water availability has been found to modify tree growth responses to N deposition in boreal and temperate conifers (Lim et al. 2015) and deciduous species (Dziedek et al. 2016). This fact is supported by modelling and forest inventory-based studies, which stated that sensitivity of forest productivity to N input depends on climate variability (Fig. 3B) (Thornton et al. 2007). It has been suggested that trees subjected to increases in N fertilization experience greater water stress (Dziedek et al. 2016, Lim et al. 2015, 2017). Nevertheless, the nature of the combined effect of N deposition and drought might vary as a function of species composition (Grossiord et al. 2014, Dziedek et al. 2016), highlighting the importance of considering species interactions when assessing the influence of GCDs on trees.

1.2.2. Tree-to-tree interactions

The response of forest productivity to GCDs is not only dependent on the physiological response of individual trees, but is greatly modified by competing neighbours and stand structure (Coomes et al. 2014, Pretzsch et al. 2016, Barbeito et al. 2017). For instance, structure and composition influence rainfall interception, runoff and water fluxes of the whole ecosystem (Aranda et al. 2012). Besides, species-specific trade-offs between water conservation and carbon uptake (e.g. Aranda et al. 2012, Silva & Anand 2013, Granda et al. 2014, Grossiord et al. 2014), as well as responses to N deposition in terms of growth, succession and mortality (e.g. Magill et al. 2004, Thomas et al. 2010) have been broadly described. Hence, the effect of combined GCDs depends on species identity and neighbourhood composition (Dziedek et al. 2016, Forrester et al. 2016).

The competitive balance between tree species is highly susceptible to environmental factors, as interactions are sensitive to phenology, physiology and relative abundances of species (Tylianakis et al. 2008). Differences in responses of different tree species to GCDs can alter competitive balances to favour certain tree species or developmental stages over others, thus affecting forest productivity and leading to spatial changes in vegetation distribution at local and regional levels (Leithead et al. 2010, Silva & Anand 2013). Projecting changes of interactions in mixed-species forest is a tough task due to the great variability of species-specific responses and the complex feedbacks among drivers and species. However, general trends have been outlined. Rising C_a may give a competitive advantage to some tree species over others, through interspecific differences in the stimulation of growth or drought resistance enhancement (Río et al. 2014a, Metz et al. 2016). Increasing drought exposure could alter the competitive hierarchy between tree species with distinct drought tolerance, resulting in shifts in tree species composition in mixed forest stands (Grossiord et al. 2014, Forrester et al. 2016). N deposition causes frequent shifts in dominance due to advantages for certain N-demanding plant species (Bobbink et al. 2010). Shifts in tree N:P ratios likely affect competitive interactions (Yuan & Chen 2015). Furthermore, changes in the competitive balance among tree species may also be mediated by altered pathogen infection rates, which are generally increased under elevated C_a, N deposition and climate warming (Tylianakis et al. 2008, Allen et al. 2010).

1.2.3. Nutrient cycling

Biogeochemical cycles of key elements such as C, N or P determine productivity, respiration and decomposition in terrestrial ecosystems (Vitousek et al. 2010, Peñuelas et al. 2013), and at the same time C storage in forest ecosystems is controlled by the biogeochemical cycles of N and P. The rate of photosynthesis is proportional to the amount and activity of the N-rich enzyme Rubisco in leaves; while P, in the form of biochemical energy and in the sugar-phosphate skeleton of DNA/RNA, is necessary for the synthesis of proteins and plant tissues (Finzi et al. 2011). Living organisms require elements in strict proportions to catalyse metabolic reactions and synthesize essential compounds with specific ratios of elements, i.e. stoichiometry of organisms (Sterner & Elser 2002). Thus, biogeochemical cycles are biologically coupled due to conserved elemental stoichiometry of plants and microorganisms that drive the cycling of C, N and P (Finzi et al. 2011). One of the most widespread hypotheses in ecological stoichiometry is the growth rate hypothesis (GRH) that links stoichiometry and growth rate (Sterner & Elser 2002). It states that organisms require relatively more investment in P-rich ribosomes and rRNA to support the rapid protein synthesis associated to fast growth thus fast-growing organisms will exhibit lower tissue N:P and C:P ratios. Although these relationships in terrestrial plants do not have conclusive results, the GRH has had consistent support in freshwater ecosystems (Sardans et al. 2012 and references therein).

Global change has drastically affected the biogeochemical cycles of C and nutrient elements of Earth's ecosystems (Vitousek et al. 1997). Rapid environmental shifts have induced the unbalance among C, N and P in plants owing to different degrees of control by biological and geochemical processes (Finzi et al. 2011, Peñuelas et al. 2012). The simultaneous changes of biogeochemical cycles and climate have striking consequences for both nutrient concentration and stoichiometric relationships of tree organs. Litterfall constitutes a major proportion of nutrient cycling between plant and soils in forests (Vitousek 1982, Presscott 2002). Thus, factors influencing amount, dynamics and composition of litterfall will determine nutrient cycling in forests. Rising C_a can increase tree C fixation and foliage biomass, whose composition is generally strongly correlated with leaf litter (Talkner et al. 2015), thus leading to decreases of plant nutrient concentrations by the so-called 'dilution effect' (Luo et al. 2006). Climatic conditions are closely linked to variations in litterfall annual production (e.g. Berg & Meentemeyer 2001, Blanco et al. 2006, Martínez-Alonso et al. 2007, Lehtonen et al. 2008, Portillo-Estrada et al. 2013), seasonal patterns (e.g. Reich & Borchert 1984, Wright & Cornejo 1990, Martínez-Alonso et al. 2007, Zhang et al. 2014) and nutrient composition (Sardans & Peñuelas 2007, Sardans et al. 2012, Matimati et al. 2014). Altered soil nutrient availability, due to impaired N and P deposition (Peñuelas et al. 2013), has been also found to modify litterfall composition through the impact on nutrient uptake and resorption processes (Aerts & Chapin 2000, Reich & Oleksyn 2004).

Stoichiometric relationships of plant tissues, and thus litterfall, undergo significant variations as a response to GCDs (Fig. 4) (Yuan & Chen 2015). Elevated C_a decreases N:P ratio as a result of decreases in plant N concentration (Sardans et al. 2012). On the contrary, warming and drought cause N:P increase due to the differential effect on N and P availability (Sardans et al. 2013, Yuan & Chen 2015). Likewise, high N deposition rates are clearly associated with N:P increases. Simultaneous GCDs have been found to generally result in additive effects on plant stoichiometry, although synergistic and

antagonistic outcomes have been reported under low and high responses, respectively (Yuan & Chen 2015).

Plants form the base of food chains, so vegetal nutrient imbalances can impact on the trophic structures and produce biodiversity losses in forest ecosystems (Güsewell et al. 2005, Bobbink et al. 2010, Peñuelas et al. 2012, 2013). Moreover, physical and chemical nature of litterfall largely determines the soil microbial activity and the resulting release of nutrients into the soil (Blanco et al. 2008), thus nutrient cycling in forests (Aber et al. 2001). Biological invasions and land-use intensification can greatly influence many components of the decomposer food web (Tylianakis et al. 2008). Forest disturbances derived from extreme events such as fires, wind storms or droughts may also have strong impacts on nutrient cycling (Dale et al. 2001).

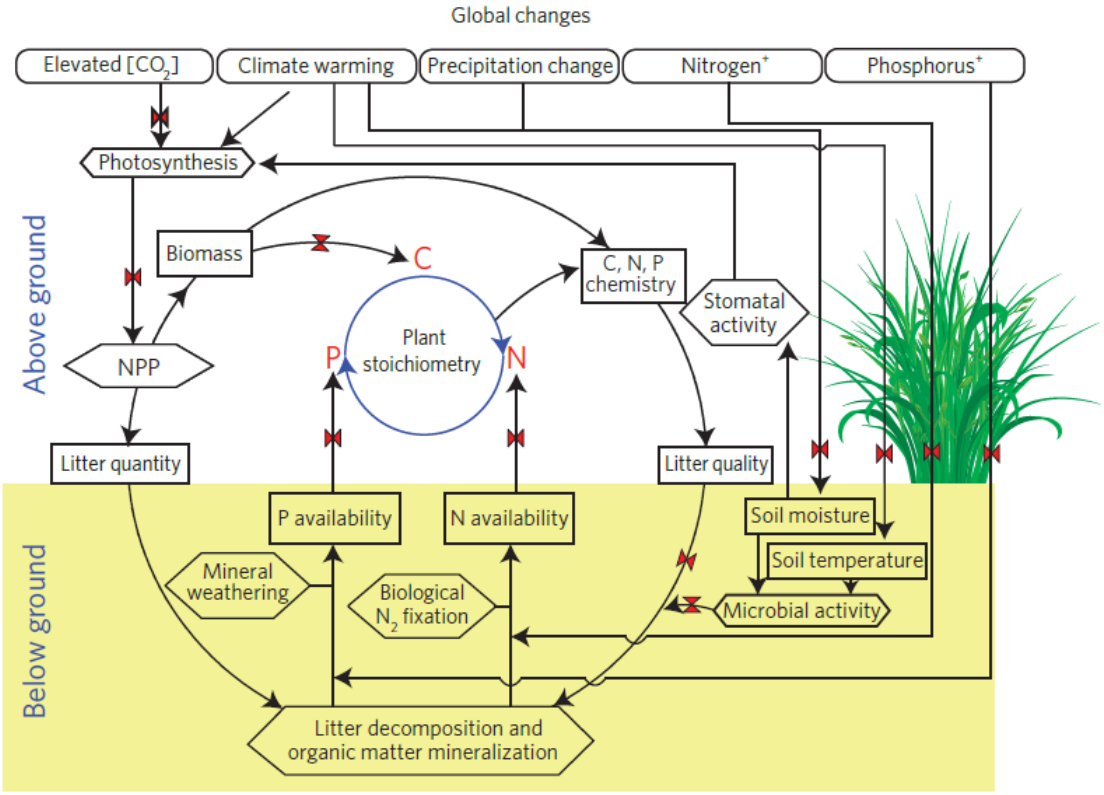


Figure 4. Conceptual framework of the impacts of global change drivers on processes controlling stoichiometry of plants. Rectangles are nutrient pools, hexagons indicate biogeochemical processes and valves (red symbols) are controls on plant C, N and P (from Yuan & Chen 2015).

2. FOREST MANAGEMENT UNDER GLOBAL CHANGE SCENARIOS

Historically, forest management has been focussed on a single dominant objective, most commonly timber production. In addition, an emphasis on increasing management efficiency by simplifying and homogenizing forest structures and operations has prevailed (Puettmann et al. 2015). However, GCDs and their interactions have boosted variability and uncertainty regarding future environmental, biological and social conditions (Puettmann 2011), together with a likely increase in the frequency and severity of disturbances and the appearance of new combinations of disturbances (Dale et al. 2001, Millar & Stephenson 2015). Increased concerns about the provision of an assortment of ecosystem goods and services have led to a shift in focus of the attention from timber towards a wide range of economic, social and ecological objectives (Kimmins et al. 2010, Ellison et al. 2017). They include conservation of biological diversity, maintenance of the productive capacity of forest ecosystems, maintenance of ecosystem health, conservation and maintenance of soil and water resources, maintenance of forest contribution to global carbon cycles, maintenance and enhancement of long-term multiple social and economic benefits, among others (McDonald & Lane 2004). Hence, forest management and silvicultural practices need to be re-evaluated as the record of historical conditions cannot provide a straightforward guide for future silvicultural practices (Messier & Puettmann 2011).

Industrial plantations are managed for maximum productivity and profitability, so mono-cultures are preferred due to the uniform nature of the trees, ease of harvesting, wood quality attributes, processing of timber, accurate yield estimates, and other industry-related reasons. Instead, forests have been proposed to be managed as complex adaptive systems, where emergent properties resulting from ecological interactions at local levels and across a variety of hierarchical scales influence adaptability to changing conditions (Puettmann et al. 2009, Messier et al. 2013, Filotas et al. 2014). It shifts the emphasis of management away from direct aspects of productivity and toward resilience and the ecosystem's ability to adapt (Millar & Stephenson 2015). As future uncertainty increases, as it has been predicted under global change, the increased emphasis on resilience and adaptation will become more important. Some silvicultural developments, such as nature-based solutions, ecosystem management, and disturbance-based approaches have been focused on diversity and heterogeneity, which are more likely to cope with new conditions when subject to unpredictable stress or disturbance, and thus have been proposed for dealing with global change (Bauhus et al. 2017a). Compared with intensive industrial plantations, these approaches have an increased emphasis on diversity regarding species mixtures, spatial scales and heterogeneous stand structures (Puettmann 2011). Several adaptation management strategies have been suggested, such as thinnings that can partially mitigate the negative impacts of more arid conditions (Primicia et al. 2013, Sohn et al. 2016, Cardil et al. 2018), or the management of forests in a mixed condition, which has been proposed to improve productivity and forest stability under climate change as will be discussed in the following section.

2.1. Mixed- species forests as adaptation strategy

Mixed-species forests are considered more resistant to disturbances and extreme events (Pretzsch et al. 2013, Neuner et al. 2015, Jactel et al. 2017) and may provide ecosystem goods and services more effectively than pure stands (Loreau et al. 2001, Gamfeldt et al. 2013, Duffy et al. 2017). There is increasing evidence of the important role of biodiversity on functioning of forest ecosystems (e.g. Hector & Bagchi 2007, Ruíz-Benito et al. 2013, van der Plas et al. 2016). The effect of biodiversity is determined by mechanistic processes directly under the influence of species interactions (Loreau et al. 2001). Physiological, morphological and phenological differences among species in mixtures can modify forest functioning as compared to pure stands (Forrester 2015, Forrester & Bauhus 2016). Interspecific interactions may lead to (i) competition for light, water and/or nutrients, (ii) facilitation (i.e. one species improves the resource availability, climatic or biotic conditions of another species), or (iii) competitive reduction also called resource partitioning (i.e. interspecific competition in the mixture is lower than intraspecific competition in pure stands) (Kelty & Cameron 1995). However, separation of the effects of facilitation and competitive reduction is extremely difficult due to the interdependence among ecological processes in mixed forests, so they are collectively described as complementarity (Loreau & Hector 2001, Forrester 2014). Competition and complementarity in mixed forests occur simultaneously, and the net effect of all of them translates into positive, neutral or negative influence on tree and stand performance as a function of the ecosystem functioning process that is being regarded.

On one hand, productivity is an important and integrative measure of ecosystem functioning (McGill et al. 2006), generally assessed when biodiversity effects on forest ecosystems are evaluated (Bauhus et al. 2017b). Overall, productivity is enhanced as tree diversity increases across major biomes (e.g. Paquette & Messier 2011, Vilà et al. 2013, Forrester & Bauhus 2016, Liang et al. 2016). Indeed, Zhang et al. (2012) in a global meta-analysis of studies comparing mixed and pure forests found 23.7 % higher productivity in mixtures. Nevertheless, this relationship is not linear but the effect declines as diversity increases (Liang et al. 2016), and it has been found to be highly dependent on other factors such as climatic factors, local conditions, stand density and evenness, stand age, functional traits involved in the mixtures, and so on (Gómez-Aparicio et al. 2011, Zhang et al. 2012, Condés et al. 2013, Silva & Anand 2013, Grossiord et al. 2014, Forrester & Bauhus 2016, Forrester et al. 2016, Madrigal-González et al. 2016, Dzikiti et al. 2016). In addition, above and belowground mixing effects may vary along spatial gradients of resource availability (Forrester 2014) and over time due to changes in resource acquisition and species interactions with stand development (Cavard et al. 2011).

The stress gradient hypothesis (SGH) predicts an increase in facilitation, and a decrease in competition, as conditions become harsher (Bertness & Callaway 1994). However, the SGH has been traditionally evaluated in agronomic studies in which facilitation is assessed comparing plants growing in communities or isolated, the latter being an uncommon situation in forests. In this context, Forrester & Bauhus (2016) proposed the "complementarity-competition" framework and the SGH as a special case of that framework. It states that when species interactions improve the availability, uptake or use efficiency of the resource that is becoming more limiting along a spatial or temporal gradient, complementarity also tends to increase along that gradient (Fig. 5) (Binkley et al. 2004, Richards et al. 2010, Forrester 2014). Several empirical researches support such theoretical background. For instance, some studies combining dendrochronological and stable isotopes of wood

of European mixtures have found that drought resistance is enhanced in mixtures as long as net water-use partitioning or water-related facilitation processes take place depending on species identity and site conditions (e.g. Grossiord et al. 2014, Forrester et al. 2016, Metz et al. 2016). Lübbe et al. (2015) and Dziedek et al. (2016) reported from sapling experiments differing responses to water stress and N fertilization as a function of the species included in the mixture, thus highlighting the importance of tree neighbour characteristics. Therefore, beneficial effects of biodiversity on forest ecosystem functioning arise only when net facilitation or resource partitioning processes occur in regard to the more limiting factor. The occurrence of such complementarity is contingent on the particular attributes of species included in a mixture or their functional traits rather than the mere tree species diversity as such (Forrester & Bauhus 2016, Bauhus et al. 2017b, Jactel et al. 2017, Vitali et al. 2018).

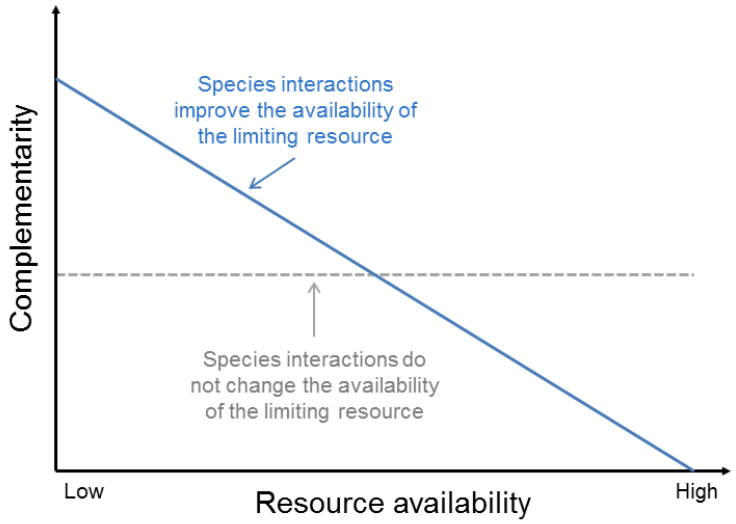


Figure 5. Representation of the theoretical "complementarity-competition" framework. Blue solid line represents increases in complementarity due to improvement of the availability, uptake, or use efficiency of the most limiting resource (i.e. light, water or nutrients) due to species interactions. Grey dash line displays the situation in which species interactions do not modify complementarity regarding the most limiting resource (from Forrester & Bauhus 2016).

On the other hand, maintenance and development of mixed forests have been identified as adaptation strategies of forest management in the face of global change (Jactel et al. 2009, 2017, Messier et al. 2013). Two different ecological mechanisms may lead to increased resistance of mixtures compared with pure forests. Firstly, the portfolio effect is related with a probabilistic component. That is, if a forest is composed of several tree species with different functional traits, there is a greater likelihood that some species are more resistant to a given abiotic or biotic disturbance, and thus improving the probability to maintain forest ecosystem functioning (Jactel et al. 2017). This goes along the same lines as the insurance hypothesis, which states that more diverse communities are expected to react less sensitively to unpredictable environmental shifts (Yachi & Loreau 1999). Secondly, complementarity and facilitation processes among different species that enhance tree and

stand resistance could emerge in mixed-species forests (Bauhus et al. 2017b). For instance, it has been proposed that drought resistance results from complementarity in belowground processes particularly root stratification (Bolte & Villanueva 2006, Grossiord et al. 2014). Such complementarity effect is not dependent on the species richness but the identity of species involved in the mixture (Grossiord et al. 2014, Dziedek et al. 2016, Forrester & Bauhus 2016, Vitali et al. 2018).

Therefore, species diversity may also increase ecological stability of forests as in mixtures the severity and duration of a disturbance could be lower, and the recovery faster or more complete than in pure stands (Bauhus et al. 2017a). Ecological stability may refer to several concepts, such as resistance, resilience or temporal stability (Ives & Carpenter 2007). The stabilization of productivity over time in diverse forests has been attributed to temporal complementarity (species asynchrony and temporal shifts in species interactions), overyielding (i.e., the productivity of mixtures is higher than the average of the pure forests), and species interactions (Isbell et al. 2009, Hector et al. 2010, Loreau & de Mazancourt 2013, Bauhus et al. 2017a). There is strong evidence that mixed forests often improve the stability of productivity, from both empirical (Jucker et al. 2014, Metz et al. 2016, Río et al. 2017) and modelling (Morin et al. 2014, Pedro et al. 2015) approaches.

2.2. European beech and Scots pine mixtures

In Europe, the light-demanding Scots pine (*Pinus sylvestris* L.) and the shade-tolerant European beech (*Fagus sylvatica* L.) are the most widely distributed conifer and broadleaf species. Although the rather continental range of the early successional conifer and the more Atlantic natural distribution range of the late-successional broad-leaved deciduous species overlap over a large area of Europe (Fig. 6), the actual area of these mixtures has been reduced owing to clearing for agriculture and they have been replaced by faster growing conifers during the last centuries. However, silviculture is paying increasing attention to mixed Scots pine – European beech forests because the complementary physiological and ecological traits of these two species may cause overyielding (Pretzsch et al. 2015a) and temporal stabilization of forest productivity (Río et al. 2017) in the face of global change.

Increased productivity in European beech – Scots pine mixtures compared to their pure stands has been reported at regional (e.g. Gabriel et al. 2005, Metz et al. 2013, Condés et al. 2013) and European scales (Pretzsch et al. 2015a), although opposite results have also been found (see Conte et al. 2018). Furthermore, significant mixing effects have been found in terms of structural heterogeneity (Pretzsch et al. 2016, Barbeito et al. 2017), light absorption (Forrester et al. 2018) and temporal stability of productivity (Río et al. 2017) of these mixtures. Different mechanisms regarding light, water and nutrient-related interspecific interactions have been proposed to drive those mixing effects. They include shifts in species allometry and stand density leading to more dense canopy packing (Pretzsch et al. 2015a, Forrester et al. 2018), contrasting vertical root distributions that contribute to a more complete belowground resource exploitation (Río et al. 2014b), temporal complementarity in intra-annual growth dynamics (Cardil et al. 2018), physiological differences regarding stomatal regulation (Hartmann 2011, Forrester 2015), interspecific differences in rainfall interception (Staelens et al. 2006, Primicia 2012, Cardil et al. 2018), or the facilitative effect of higher litter quality

of European beech that promotes higher litter decomposition rates and thus faster nutrient cycling (Perry et al. 1987, Blanco et al. 2008, 2011).

In addition, Scots pine and European beech are vulnerable to quite different disturbances, which increases the probability that a given disturbance affects less strongly any of the species so these mixtures would more likely maintain their functioning, that is, mixed forests would exhibit higher resilence relative to pure stands (Bauhus et al. 2017a). The high sensitivity of European beech to water deficit (Geßler et al. 2007) might be partly alleviated by the presence of Scots pine due to intraspecific competition release (Condés et al. 2013, Río et al. 2014a). Likewise, Scots pine would also likely obtain benefits from the admixture of beech from the mitigation of the susceptibility to secondary stress made by insects, fungi, or windthrow damage caused by drought (Allen et al., 2010). Therefore, Scots pine – European beech mixtures are less associated with catastrophic events than their respective pure stands (Kint et al. 2006).

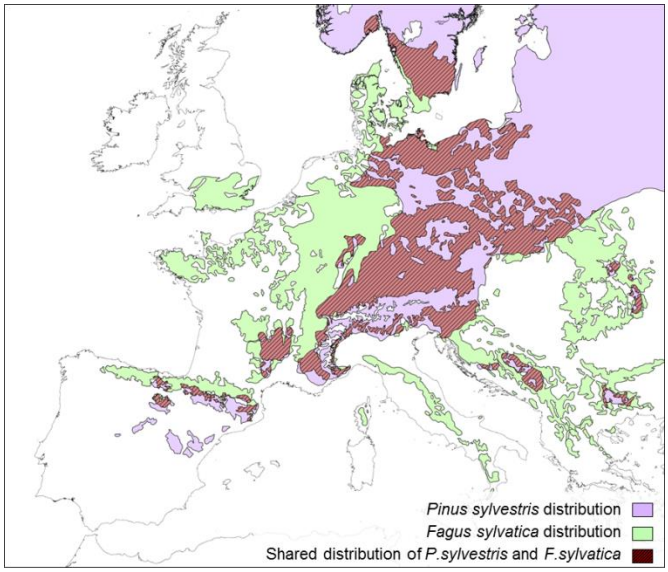


Figure 6. Natural distribution of Scots pine (*Pinus sylvestris*) and European beech (*Fagus sylvatica*) (EUFORGEN 2009), and the common area between both species.

Mixing effects in European beech-Scots pine stands have been shown to vary along water availability gradients (Pretzsch et al. 2016) and the lack of significant relationships between overyielding and site index or climate variables suggests that different mechanisms promote complementarity depending on environmental conditions and stand development stage (Pretzsch et al. 2015a). As the climate in continental Europe is projected to shift towards warmer and drier conditions in the South, and warmer and wetter summers in the North (IPCC 2013), there is a potential for the range of Scots pine to expand northwards and upwards in elevation. In contrast, European beech is expected to migrate towards higher elevations but to decline in lower and mid altitudes, where it could be replaced by pine or other species (Peñuelas & Boada, 2003). The Iberian Peninsula represents the southern and western limits of the range of both Scots pine and European beech (Fig.

6). Accordingly, this region is likely to be highly sensitive to climate change. Besides, mountain ranges of the north-eastern Spain have been identified to be under saturation risk due to N deposition (García-Gómez et al. 2014). Hence, an analysis of the potential impacts of the shift in environmental conditions as a consequence of global change on these rear-edge forests will provide valuable insights towards understanding long-term impacts of warmer and/or drier conditions throughout the broader range of these species.

3. MODELLING MIXED-SPECIES FORESTS RESPONSES TO GLOBAL CHANGE

The scarcity or lack of long-term empirical data of forest stand dynamics covering the whole lifespan of forest stands makes forest growth models a valuable means for understanding and predicting ecosystem functioning and they are a useful decision-support tool in forest management. Forest models are abstractions of the natural dynamics of a forest stand, and may encompass growth, mortality and other changes in stand composition and structure (Vanclay 1994). From the initial first experience tables to the following yield tables, then diameter distribution models and lately tree- or organ-level models, forest models have evolved getting more complex as scientific knowledge and computational power have advanced (Porté & Bartelink 2002, Kimmins et al. 2008). They are often classified into empirical, process-based and hybrid models. Empirical or statistical models rely on the collection and analysis of data that characterize the stand so statistical variability of parameters can be estimated. Process-based models attempt to mechanistically represent physiological processes that influence growth and how these processes are influenced by the environment. Hybrid models are based on physiological principles as much as possible, while relying on allometrics and other accepted statistical modelling conventions for the remainder of the attributes of interest (Kimmins et al. 1999, Weiskittel et al. 2011). Forest models are also defined as a function of their spatial and temporal resolution. Models that operate at tree, organ or cell levels and in time steps of minutes and hours are commonly referred as 'bottom-up' and offer a high resolution, although they can produce significant errors when scaling up to stand level. On the contrary, stand-level approaches (sometimes called 'top-down') usually integrate the effect of forest functioning drivers into annual scale outputs, even if they do not consider processes at the resolution on which they actually occur (Duursma & Medlyn 2012, Pretzsch et al. 2017).

When modelling mixed-species forests, empirical models often assume that dynamics of mixtures are the weighted mean of pure stands. Thus, mixing effects are either not considered and/or not allow changing from site to site or as stands develop (Pretzsch et al. 2015b). However, in view of the increasing instability in forest ecosystems due to global change (see section 1) together with the evidence of mixing effects on forest functioning (see section 2), models for mixed forests need to present those features. Different approaches in empirical modelling have been developed trying to solve these issues, such as the use of competition indices or multipliers. However, competition indices approach models competition in relation to available space rather than in terms of resource availability or environmental conditions, whereas the use of modifiers needs observational data for calibration and are typically restricted to a narrow range of conditions (Landsberg & Waring 1997, Porté & Baterlink 2002, Landsberg 2003, Pretzsch et al. 2017).

Instead, process-based models simulate the effects of interactions by calculating the availability and uptake of resources for each tree or cohort considering species-specific spatial structure and physiology and environmental conditions (Kimmins et al. 1999, Forrester & Tang 2016). The mechanistic reproduction of mixing effects in models requires a description of the relevant processes for tree growth and carbon allocation, such as light interception, photosynthesis, respiration, transpiration, nutrient uptake and allocation, mortality, and availability of soil nutrients and water content, among others. Therefore, these properties make process-based models a suitable tool for understanding and predicting shifts in mixing effects in relation to resource availability gradients, stand density, species proportions and spatial structures (Porté & Baterlink 2002, Weiskittel et al. 2011, Río et al. 2014b, Blanco et al. 2015, Pretzsch et al. 2015b).

Nevertheless, process-based mechanistic models require a high demand for calibration data and imply a strong calibration effort, which could hinder its applicability in forest management in addition to scientific and educational purposes (Blanco et al. 2007, Kimmins et al. 2008). One solution to to improve suitability of empirical approaches to model novel mixtures in a changing environment and to the calibration challenges posed by process-based models may lie in hybrid models, which combine the short term accuracy of the empirical models with the predictive power and flexibility of mechanistic approaches (Kimmins et al., 1999; Landsberg, 2003, Blanco et al. 2015). Moreover, they usually reduce error propagation when scaling up to stand level and sometimes even provide better growth predictions than empirical models developed for the same regions (Forrester & Tang 2016).

The versatility of a forest model for both research and management objectives is its portability (i.e. the ease with which a model can be calibrated and applied to an ecosystem different from that in which it was originally developed). Despite the increasing volume of published forest growth models during the last decades, especially after 1990, only a few ones have been applied outside their developing team in different countries and biomes (Blanco et al. 2015). They include, among others, the gap-type FORMIND (Fischer et al. 2016) and FORMIX (Bossel & Krieger 1991, Huth et al. 1996) models originally developed to simulate tropical forest dynamics, the individual-tree spatially explicit SILVA model (Prestzsch et al. 2002), and the ecosystem-level model FORECAST that operates at stand-scale (Kimmins et al. 1999, Seely et al. 2015). Of the above, FORECAST is the most ecologically diverse model as it has been successfully applied in different biomes, including temperate and subboreal forests (Blanco et al. 2007, Seely et al. 2015), subtropical mixed plantations (Dordel et al. 2011, Wei & Blanco 2014) and Mediterranean montane forests (Lo et al. 2015, González de Andrés et al. 2017).

In FORECAST, the rates of the key ecological processes driving tree growth are calculated from historical bioassay data and measures of certain ecosystem variables (e.g., decomposition rates and photosynthetic saturation curves) and their relation to nutrient uptake, the capture of light energy and net primary production (Kimmins et al. 1999). This hybrid approach reduces calibration requirements while ensuring that productivity projections are reasonable (Blanco et al. 2007). This model uses a mass balance approach to simulate nutrient cycling and includes a hydrological module in its latest version (FORECAST Climate, Seely et al. 2015), which provides a mechanistic representation of above- and belowground hydrological interactions in forest stands with multiple soil and canopy layers (Seely et al. 2015). As simulated tree growth is limited by available light, water

and nutrients, site conditions may change during stand simulation, and different climate and management scenarios can be modelled, FORECAST seems to be an appropriate forest model to assess species interactions in mixtures under changing conditions.

Based on the previous premises, the versatility of using a combination of modelling, empirical and statistical approaches to study the relationships between different limiting factors in mixed forests of European tree species growing at their southern distribution limits is tested in the research reported in this PhD thesis.

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GENERAL AIM

GENERAL AIM

Mixed-species forests are receiving increasing attention due to their potential benefits in terms of productivity and adaptation to global change. Although the scientific knowledge of the structure and functioning of mixtures is rapidly growing, there are still many knowledge gaps about mixing effects and their variation along spatial and temporal gradients required for understanding the functioning of mixed forests and for designing adaptive management plans that ensure the supply of a wide range of ecosystem goods and services.

In Europe, the study of the widespread European beech-Scots pine mixtures may serve as a model system for other species combinations with comparable functions. This thesis research is focused on mixed forest stands of European beech and Scots pine of the southwestern Pyrenees in the province of Navarre (northern Spain), where the Ecology and Environment Research Group of the Universidad Pública de Navarra has been monitoring diverse forest processes related to tree growth, nutrient cycling, biodiversity and their interactions in a set of experimental plots since 1999. Those forests represent the southern and western limits of the range of both species and therefore constitute a unique opportunity to study the responses of rear-edge populations to changes in environmental and biological conditions that will also impact areas in the central portion of their distributions. Two contrasting sites have been considered: a sub-xeric site located at low elevation with a cool and dry Mediterranean climate, and a mesic site situated at high elevation and characterized by cold-wet continental climate. Both forests are even-aged Scots pine stands resulting from successful natural regeneration after clear-cuttings carried out in the early and mid-1960s. Over recent decades, European beech growth under pine canopy has progressively resulted in mixed stands, particularly at the Mediterranean site.

The main objective of this thesis research is to assess natural ecological succession towards Scots pine – European beech mixed stands, and to evaluate the influence of species interactions on forest processes and predict their possible responses in relation to shifts in resource availability and environmental conditions as a consequence of global change. Two main hypotheses are raised in this research. Firstly, water availability is the primary influence on ecosystem functioning within mixed European beech – Scots pine forests of the southwestern Pyrenees, due to both direct and indirect effects of water shortage on tree physiology and nutrient cycles. Secondly, the complementarity between species will increase as water becomes more limiting as long as species interactions improve availability, uptake or use efficiency of water.

Within this general objective, the following specific objectives were defined and addressed in three different chapters. The first chapter evaluates the combined effect of rising atmospheric CO_2 concentration, intra- and interspecific competition and climate on secondary growth and intrinsic water-use efficiency (iWUE) at tree-level using dendrochronological techniques and the analysis of stable carbon isotopes' composition. The relationship between growth and WUE is also assessed to test if drought-related growth declines can be compensated by increases in WUE. In the second chapter the forest growth ecosystem-level model FORECAST Climate is used to simulate stand development of European beech – Scots pine mixtures growing under the conditions of the

southwestern Pyrenees in order to analyse the underlying causes of complementarity and competition between both tree species. Simulations under projections of climate change for the next century are carried out with the aim of providing a prediction of the species mixing trends in these rear-edge populations. Finally, the third chapter studies the influence of local climate and large-scale atmospheric-oceanic patterns on production, seasonality and nutrient composition of leaf litter series collected during autumn over a 16-year period in the two contrasting mixed stands. Temporal series of nutrient concentration and stoichiometry are used as proxies for nutrient inputs within the stands. In addition, the relationship among leaf litter dynamics and secondary growth and WUE of Scots pine trees is assessed.

Therefore, a multidisciplinary methodology is employed to test the previous hypotheses by comparing different processes of forest functioning such as water-use efficiency, tree growth or aboveground litterfall dynamics between the two study sites. The study uses a multi-scale approach regarding two different issues. Firstly, two different levels of ecosystem organization are analysed: tree (Chapter 1) and ecosystem levels (Chapters 2 and 3). Secondly, climatic factors influencing forest functioning are of local nature at first and second chapters, while a global component is introduced at the third chapter as large-scale atmospheric-oceanic circulation patterns are added to the analyses.

CHAPTER 1

Tree-to-tree competition in mixed European beech – Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions

Tree-to-tree competition in mixed European beech-Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions

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ABSTRACT

Mixed conifer-hardwood forests can be more productive than pure forests and they are increasingly considered as ecosystems that could provide adaptation strategies in the face of global change. However, the combined effects of tree-to-tree competition, rising atmospheric CO_2 concentrations and climate on such mixtures remain poorly characterized and understood. To fill this research gap, we reconstructed 34-year series (1980-2013) of growth (basal area increment, BAI) and intrinsic water-use efficiency (iWUE) of Scots pine (*Pinus sylvestris* L.) – European beech (*Fagus sylvatica* L.) mixed stands at two climatically contrasting sites located in the southwestern Pyrenees. We also gathered data on tree-to-tree competition and climate variables in order to test the hypotheses that (i) radial growth will be greater when inter-specific competition exceeds intra-specific competition, i.e. when species complementarity occurs, and (ii) enhanced iWUE could be linked to improved stem radial growth. Growth of both species was reduced when intra-specific competition increased. Species complementarity was linked to improved growth of Scots pine at the continental site, whilst competition overrode any complementarity advantage at the drought-prone Mediterranean site. Beech growth did not show any significant response to pine admixture likely due to shade tolerance and the highly competitive nature of this species. Increasing inter-specific competition drove recent iWUE changes, which increased in Scots pine but decreased in European beech. The iWUE enhancement did not involve any growth improvement in Scots pine. However, the positive BAI-iWUE relationship found for beech suggests an enhanced beech growth in drought-prone sites due to improved water use.

Key words: basal area increment, drought, *Fagus sylvatica*, *Pinus sylvestris*, biotic interactions, stable carbon isotopes, atmospheric CO_2 concentration.

1. INTRODUCTION

Over the past two centuries, many anthropogenic influences on the global carbon (C) biogeochemical cycle have been reported (Francey et al. 1999). The major human influence on the C cycle is the rapid rise of atmospheric CO_2 concentration (C_a) due to fossil fuels burning and other anthropogenic activities, leading to substantial increases in air temperatures over many regions and to an altered distribution of rainfall in some of them (IPCC 2013). The occurrence of increased C_a coupled with more frequent and intense dry spells in some areas, as in drought-prone southern Europe, is affecting trees´ gas-exchange metabolism, water use and radial growth (Peñuelas et al. 2008, Andreu-Hayles et al. 2011). In controlled experiments, increased C_a enhances trees' photosynthesis and reduces stomatal conductance (Mousseau & Saugier 1992; Norby et al. 1999). As a consequence, intrinsic water-use efficiency (iWUE; i.e. the ratio of assimilated C to transpired water) and growth are expected to increase (Farquhar et al. 1989, Huang et al. 2007). In contrast, decreases in soil water potential due to drought can reduce trees' photosynthetic C uptake as trees close stomata to prevent hydraulic dysfunction (Körner 2000).

Thus, on one hand, rising C_a can increase iWUE and improve trees' ability to withstand dry conditions. On the other hand, stomatal closure induced by drought could cancel out any potential growth benefit from C_a increase (Körner 2000; Huang et al. 2007). Moreover, a progressively diminishing tree response to increasing C_a and a decoupling of growth and iWUE have been reported (Waterhouse et al. 2004, Linares et al. 2009, Peñuelas et al. 2011). Therefore, assessments of the growth-iWUE relationship in natural forests are necessary to predict future forest responses to combined rising C_a and warmer conditions in areas subjected to seasonal droughts (Körner 2000, Boisvenue & Running 2006). Several studies have revealed that trees vary in their response to increasing C_a, often showing improved iWUE but not enhanced growth, and thus reduced water use, which points to species-specific responses (Lévesque et al. 2014), and influences of availability of other resources (Warren et al. 2001).

Tree-rings are a valuable tool to reconstruct long-term effects of environmental variables on growth, and their C isotope ratio ($^{13}C/^{12}C$) can provide an insight into trees' iWUE for the period when the ring was formed (Farquhar et al. 1989, McCarroll & Loader 2004). Most research has focused on the relationship between tree-ring variables (e.g. tree-ring width, $\delta^{13}C$ or iWUE), climatic factors, and rising C_a. However, such studies have been focused on freely growing, dominant or isolated trees, whereas interactions among neighbouring trees have not been often analysed despite the well-known fact that trees compete for light, water, and other resources. In fact, the effects of such interactions may be more important than climate factors (Linares et al. 2009, Primicia et al. 2013, Fernández-de-Uña et al. 2016). Previous studies have shown a common trend that indicates an evident negative effect of increased competition on growth (e.g. McDowell et al. 2006, Martín-Benito et al. 2010, Primicia et al. 2013), whilst the effects on iWUE depend on whether C assimilation or stomatal conductance is more strongly affected by trees' competition (Fernández-de-Uña et al. 2016, and references therein).

Nowadays, species mixtures are receiving increasing attention because they can be more productive than pure stands. Therefore, mixing tree species has been identified as an adaptation

strategy in forest management to cope with climate change (e.g. Zhang et al. 2012, Forrester 2015, Pretzsch et al. 2015, González de Andrés et al. 2017). In mixed stands, growth and drought response of trees are altered by both intra- and inter-specific competition. Inter-specific differences in physiology, phenology or morphology can modify iWUE and growth of mixed stands as compared to pure stands (Forrester 2015, Forrester & Bauhus 2016). Hence, species interactions may promote net competition, facilitation (i.e. one species improves the resource availability, climatic or biotic conditions of another species) or competitive reduction (i.e. inter-specific competition in the mixture is lower than intra-specific competition in the pure stands) (Kelty & Cameron 1995). In this sense, the identity of the competing neighbours has a strong influence on the interaction effects among trees. Therefore, each species combination should be considered when studying competition and environmental impacts on mixed stands performance. The inter-dependence among ecological processes in mixtures makes extremely difficult to separate the effects of facilitation and competitive reduction, so both interaction types have been described collectively as complementarity (Loreau & Hector 2001). The assessment of such complementarity concept in terms of growth and iWUE changes can provide valuable insights towards understanding drought sensitivity of trees in mixed stands.

Here we focus on the interactions between a light-demanding conifer (Scots pine, *Pinus sylvestris* L.) and a shade-tolerant broadleaf (European beech, *Fagus sylvatica* L.). Although mixtures of beech and pine have been observed to provide an overall increase in yield of 12 % in comparison with pure stands (Preztsch et al. 2015), there is a scarcity of knowledge on the physiological mechanisms that can favour species complementarity. They are the most widely distributed conifer and broadleaf tree species in Europe. Their distributions overlap over a large area of the continent and the Iberian Peninsula represents the south-western distribution limits of both species (Fig. S1 in Appendix A). In addition, this region is likely to be highly sensitive to climate change, as it has been predicted an increase in the frequency and severity of drought events (IPCC 2013). Therefore, the Iberian Peninsula could be one of the first regions where growth-related features of both species would be altered by climate change.

Primicia et al. (2013) reported a higher sensitivity of Scots pine growth to temperature and precipitation in thinned than in unthinned plots in the south-western Spanish Pyrenees. The same authors also highlighted the influence of the identity of the competing neighbours in sensitivity responses to climate. The importance of competition on the response of beech to environmental factors has been also reported in "core" areas of the species distribution, such as central Europe (Metz et al. 2016). Hence, an analysis of the physiological mechanisms underlying species interactions on rear-edge populations, located close to the species' southern limit of distribution, will contribute to understand current patterns in tree growth and iWUE in pine-beech mixtures and to predict their future response to climate change throughout the broader range of these species.

Since intra- and inter-specific competition dynamics can be managed to minimize the negative effects of droughts associated with climate change on tree physiology and growth, we aimed to assess the ecological relevance of competition as a potential constraint on iWUE and growth for Scots pine and European beech in mixed stands of the western Spanish Pyrenees. Our specific objectives were: 1) to evaluate the differential effects that competition, rising C_a trends and climate exert on iWUE and

growth of pine and beech trees, 2) to relate iWUE to growth changes, and 3) to test whether possible increases in iWUE linked to rising C_a can compensate the negative effects of drought on growth of both species. We hypothesized that: 1) trees' radial growth is greater when exposed to inter- than to intra-specific competition when species interactions improve the availability of a limiting resource (following the 'complementarity – competition' framework *sensu* Forrester & Bauhus 2016), and 2) increases in iWUE would enhance radial growth due to improved photosynthesis with lower water loss which is advantageous to face water shortage. To test these hypotheses we employed a combination of dendrochronological tools and measurements of carbon isotope composition to evaluate iWUE and growth trends of pine and beech mixtures at two climatically contrasting sites.

2. MATERIALS AND METHODS

2.1. Study area and climatic data

The study area is located in the south-western Pyrenees, northern Spain (province of Navarre; Fig. S1). In this region, beech is limited to the northern slopes and valley bottoms with deep soils, while Scots pine usually appears in southern and dry slopes. Management plans together with abandonment of former pastures have favoured Scots pine, replacing the pre-existing oak and beech forests (Loidi & Báscones 1995). However, over recent decades, mixed stands have been encouraged by allowing beech growth under pine canopy (MMA 2002). Two contrasting sites were sampled: a sub-xeric site located at low elevation with a cool and wet Mediterranean climate (Aspurz), and a mesic site situated at high elevation and characterized by cold-wet continental climate (Garde). Apart from Scots pine and beech, other overstory tree species identified in the pine-dominated plots were *Quercus humilis* L., *Q. ilex* L. and *Ilex aquifolium* L. at the Mediterranean site, whereas only the latter is present at the continental site. In the case of the beech-dominated plots, *I. aquifolium*, *Buxus sempervirens* L., *Populus nigra* L. and *Acer campestre* L. were the main non-target woody species at the Mediterranean site. No significant presence of any other tree species was found in the beech-dominated plots at the continental site. Data describing soil characteristics were obtained by digging soil pits from each site. Further information on sites' characteristics and stands' structure is provided in Table 1.

In order to evaluate the impact of climatic conditions on growth and isotope series, historical climate data for the period 1980-2013 were obtained from the nearest weather stations to each site. Due to the large elevation difference between the continental site and the closest weather station (over 600 m), the mountain microclimate simulation model MT-CLIM (Running et al. 1987) was applied to correct climate data (Lo et al. 2011). Maximum and minimum temperature lapse rates and precipitation isohyets needed for extrapolation were calculated from regional climate data. Missing data were calculated by interpolating values from nearby weather stations.

Table 1. Sites and stands characteristics (mean ± standard error) measured in 2014. Stands descriptors were taken from Puertas (2001) and Iriarte and Puertas (2003).

Site	**Mediterranean warm-dry site (Aspurz)**		**Continental cold-wet site (Garde)**	
Altitude (m a.s.l.)	625		1335	
Climate type (Papadakis, 1970)	Cold wet Mediterranean		Cold wet continental	
Mean annual temperature (º C) [a]	11.9 ± 0.1		9.4 ± 0.1	
Total annual precipitation (mm) [a]	922 ± 25		1346 ± 61	
Soil	Haplic Alisol		Dystric Cambisol	
Soil depth (cm) [b]	93.8		79.7	
CEC (cmol+ kg^{-1}) [c]	14.6		12.6	
Maximum field capacity (%)	38.8		38.8	
	Scots pine stands	**Beech stands**	**Scots pine stands**	**Beech stands**
Slope (%)	7	37	40	45
Density (stems ha^{-1}) [d]	2400 ± 301	995 ± 105	2019 ± 212	982 ± 185
Basal area (m^2 ha^{-1})	57.5 ± 2.25	47.2 ± 6.1	56.0 ± 6.3	30.6 ± 8.1
Tree species richness	18	7	10	3
Density proportion of *P. sylvestris* (%)	69.34 ± 0.02	24.63 ± 0.10	85.22 ± 0.06	12.78 ± 0.06
Density proportion of *F. sylvatica* (%)	11.73 ± 0.04	64.16 ± 0.09	13.71 ± 0.05	87.22 ± 0.06
Site Index at stand age 80 years (m) [e]	29	21	23	18
Age (years) [e]	47	72	51	38
Dominant height (m) [e, f]	20.4 ± 0.3	17.3 ± 0.8	17.3 ± 0.9	13.2 ± 0.5
Mean dbh (cm) [e, g]	17.2 ± 1.1	15.5 ± 1.5	17.9 ± 0.8	13.0 ± 1.1
$DCI_{intra\text{-}sp}$ [h]	6.59 ± 0.49	2.02 ± 0.49	6.16 ± 0.59	1.94 ± 0.42
$DCI_{inter\text{-}sp}$ [h]	1.04 ± 0.13	1.38 ± 0.25	0.28 ± 0.14	0.46 ± 0.19

[a] Referred to the period 1980-2013.
[b] Sum of horizons O, A and B.
[c] Average value between horizon A and horizon B.
[d] Trees with a diameter at breast height (1.30 m, dbh) > 7.5 cm.
[e] Referred to plots' dominant species (*P. sylvestris* in Scots pine stands and *F. sylvatica* in beech stands).
[f] Measured averaging (n = 100) the height of the thickest dominant trees per hectare.
[g] Measured by double cross measurement.
[h] Hegyi's (1974) distance-dependent competition index (*DCI*) was calculated following Eq. 5. Presented values correspond to all neighbouring trees within a fixed radius plot of R = 9 m from the focal tree in Scots pine stands, and R = 5 m in beech stands. Values are calculated as the average competition experienced by trees during the period 1980-2013.

The 0.5º-gridded CRU TS 3.22 data set produced by the Climate Research Unit (University of East Anglia) was used to complete the climate data series from the date of birth of the oldest trees (1920) until 1980 (Harris et al. 2014). As CRU series are based on average elevation of their corresponding 0.5º grid, linear regressions between CRU and local weather station series (see above) were made for the common period 1980-2013 and the correction was applied to CRU data from 1920 to 1980 to obtain adjusted climate series for the study sites. Water balance was obtained from the sum of monthly differences between precipitation data and potential evapotranspiration (PET). PET was estimated following Thornthwaite & Mather (1957). Seasonal values of climate variables were calculated from monthly data: previous autumn (September to November prior to the year of tree-ring formation), winter (previous December to February), spring (March to May), and summer (June to August). Temporal trends in annual and seasonal temperatures and water balance were calculated by using linear simple regressions. Since 1920, annual temperatures have significantly risen ($P < 0.001$) at both study sites with a rate *ca.* +0.020 ºC year^{-1} (Fig. S2A). Water surplus showed a significant decreasing trend at both sites ($P < 0.001$), which was more pronounced in the Mediterranean site (Fig. S2B). These trends were also present at seasonal level for temperature (all seasons, both sites) and water balance (spring and winter, both sites) (results not shown).

2.2. Field sampling and dendrochronological procedures

At each location, three plots dominated by Scots pine (30 m x 40 m) and three plots dominated by European beech (20 m x 20 m) were set up and diameter at the breast height was measured (dbh, measured at 1.30 m height) for every tree inside the plots (Table 1). We randomly chose eight dominant and co-dominant trees per plot (n = 98, 50 pine trees from the pine-dominated plots and 48 beech trees from the beech-dominated plots) to obtain a representation of stand historical growth (Lo et al. 2010). Selected trees were sampled at breast height perpendicular to the maximum slope using a Pressler increment borer. Two complete radii were extracted from each tree. Cores were air dried, glued onto wooden mounts and sanded until tree rings were clearly visible (Fritts 2001). All samples were visually cross-dated using the identification of signature years. Tree-ring width was measured to a precision of 0.01 mm using a LINTAB measuring device (Frank Rinn, Heidelberg, Germany). Cross-dating was further validated using the COFECHA software, which calculates moving correlations among individual tree series (Holmes 1983). For each tree, measurements from the two cores were averaged. In those cases when tree cores did not reach the pith, the distance to the theoretical centre of the stem was estimated by fitting a template of concentric circles to the curve of the innermost rings (Norton et al. 1987). These geometric corrections were used to estimate the age at 1.30 m of all trees. For each tree, measurements from the two cores were averaged as they were considered as replicates. We transformed tree-ring width series into annual basal area increment (BAI) using the following formula and assuming concentric rings:

$$BAI = \pi (r_t^2 - r_{t-1}^2) \quad \text{(Eq. 1)}$$

where r_t and r_{t-1} are the radii corresponding to years t and $t-1$, respectively. We used BAI because it is a more biologically meaningful expression of growth than tree-ring widths or indices, since BAI

displays a young exponential phase and reaches an asymptotic phase when trees reach a mature stage (Biondi & Qaedan 2008).

2.3. Tree-ring isotopes analysis and water-use efficiency

Stable C isotopes in tree rings provide useful proxies of long-term changes in iWUE (McCarroll & Loader 2004). Isotopic discrimination in C3 plants is a result of the preferential use $^{12}CO_2$ over $^{13}CO_2$ during photosynthesis. The two stable C isotopes are incorporated in varying amounts depending on the ratio between the intercellular (C_i) and the atmospheric CO_2 concentrations (C_a). For example, if a drought event occurs, stomatal conductance will decrease relative to the rate of photosynthesis, and the diminished C_i will cause less discrimination against ^{13}C (Farquhar et al. 1989).We used $^{13}C/^{12}C$ isotope ratios in wood from cross-dated cores as proxies of the iWUE. We randomly chose five trees of each species at each study site (n = 20, 10 pine trees and 10 beech trees) among trees previously selected for growth analysis. We extracted two additional radii from these trees: 5-mm thick cores that were used as a support to cross-date 10-mm thick cores used for C isotope analyses. The 5-mm cores were prepared following dendrochronological methods as explained before. The 10-mm thick cores were cross-dated and tree rings (including earlywood and latewood) were separated manually from the cores using a scalpel under a stereomicroscope. The samples were milled to a fine powder using a ball mill (Retsch ZM1). We used intact wood tissue for C isotope analyses as both whole wood and cellulose isotope time-series show similar long-term trends related to atmospheric CO_2 and climate (Saurer et al. 2004, Ferrio & Voltas 2005). The $^{13}C/^{12}C$ ratios of wood samples were determined by mass spectrometry using a Flash EA-1112 elemental analyser interfaced with a Finnigan MAT Delta C isotope ratio mass spectrometer at the Stable Isotope Facility (University of California, Davis, USA). The standard deviation for the repeated analysis of standard cellulose was better than 0.1‰ for C. The results were expressed as isotopic composition ($\delta^{13}C$) relative to the standard Vienna Pee Dee Belemnite (VPDB) (IAEA 1995) following Eq. 2.

$$\delta^{13}C\ (‰) = [(R_{sample} / R_{standard}) - 1] \times 1000 \qquad \text{(Eq. 2)}$$

in which R_{sample} and $R_{standard}$ represent the $^{13}C/^{12}C$ ratios of the sample and the VPDB international standard, respectively (Farquhar, O'Leary & Berry 1982).

Following Farquhar, O'Leary & Berry (1982) we estimated iWUE using Eq. 3.

$$\text{iWUE} = A / g = C_a\,[1 - (C_i / C_a)]\,0.625 \qquad \text{(Eq. 3)}$$

where A is the rate of net photosynthesis, g is stomatal conductance to H_2O, and 0.625 is the relation among conductance of H_2O and CO_2. To determine C_i, we used the following equation proposed by Francey & Farquhar (1982) (Eq. 4).

$$C_i = C_a\,[(\delta^{13}C_{plant} - \delta^{13}C_{atm} + 1) / (b - a)] \qquad \text{(Eq. 4)}$$

where $\delta^{13}C_{plant}$ and $\delta^{13}C_{atm}$ are the plant and atmospheric C isotope compositions, respectively, a is the diffusion fractionation across the boundary layer and the stomata (+4.4 ‰), and b is the Rubisco enzymatic biologic fractionation (+27.0 ‰). The long-term C_a and atmospheric $\delta^{13}C$ from 1923 (oldest

tree-ring in all samples) to 2003 were obtained from McCarrol & Loader (2004). Additional data (from 2004 to 2013) for C_a and $\delta^{13}C$ were taken from the Earth Research Laboratory website (http://www.esrl.noaa.gov/).

2.4. Beech response to rising atmospheric CO_2 concentration

Due to the uneven age distribution of beech in the Mediterranean site, additional sampling of trees born before and after 1950 (n = 10) was performed at this site. That date was chosen as a turning point because C_a steeply rose after 1950 owing to the accumulated effects of the industrial revolution (which started *ca.* 1850). Two radii were extracted from each tree. The first core was prepared for assessing changes in growth and estimating BAI following dendrochronological methods as explained before. The 30 innermost tree-rings of the second core were separated at a 5-year resolution and then milled. The $^{13}C/^{12}C$ ratio of wood samples was determined and the iWUE values calculated. See section 2.3 for further details.

2.5. Competition index

The spatial position of every tree with a dbh larger than 2.5 cm within each experimental plot was measured. The degree of competition around each sampled tree was assessed using Hegyi's (1974) distance-dependent competition index (*DCI*). This index is derived from the hypothesis that the competitive effect of a neighbour tree increases with increasing size and proximity (Tomé & Burkhart 1989). The competition caused by tree *j* on focal tree *i* was calculated as the ratio dbh_j/dbh_i divided by the distance between tree *i* and tree *j* ($dist_{ij}$), summed over all *j* neighbouring trees within a radius *R* of tree *i* (Eq. 5).

$$DCI = \Sigma\ [(dbh_j/dbh_i) \times (1/\ dist_{ij})] \qquad \text{(Eq. 5)}$$

In order to calculate *DCI* values prior to the sampling date, the diameters of all trees in the plots were reconstructed. Ring widths of cored trees were multiplied by two to obtain annual diameter increments. Diameter increments were fitted against measured diameter in 2013 (dbh_{2013}) and year of ring formation using linear models for each site and each species. Based on the adjusted equation we estimated annual diameter increment of non-cored trees, which was sequentially subtracted to their dbh_{2013} to reconstruct dbh of all trees for the period 1980-2013. Although such approach leaves out those trees that died during stand development and were therefore not detected during the inventories and sampling, such trees are mostly sick and dominated individuals with small root systems, which had little effect on nutrient competition (Blanco et al. 2006, 2009). Not accounting for such small trees has been proven not significant for the performance of distance-diameter indexes as predictors of tree growth (Lorimer 1983). The competing neighbours were determined by the fixed-radius method. The *DCI* values were obtained using neighbourhood radii ranging 1 to 15 m (in 1 m increments) from the focal tree and these values were fit against mean iWUE of each sampled tree. Then, the distance with the highest coefficient of determination (R^2) was chosen, and the corresponding *DCI* was used in subsequent analyses. For each tree the *DCI* was divided into inter-specific and intra-specific competition *DCI*s when trees of different species from the focal tree species ($DCI_{inter\text{-}sp}$) and trees of the focal species ($DCI_{intra\text{-}sp}$) were considered, respectively.

2.6. Statistical analysis

Temporal trends in isotope data ($\delta^{13}C$ and iWUE) were assessed through linear mixed-effects models (LMMs). Tree nested in plot was included as a random effect, as well as a first-order autocorrelation structure to account for the repeated measures on the same tree (Zuur et al. 2009). We included as fixed factors "Year" and the interaction "Year x site" to detect differences in the rates of change between populations in each location for the same species, and the interaction "Year x species" to test differences between species. The correlation between each $\delta^{13}C$ series and a master chronology built from all the other series was also calculated.

LMMs were used to assess the effect of environmental variables (competition status, C_a, climate), cambial age (the age of the tree when the ring was formed), site, and their interactions on iWUE and growth (BAI) trends for the period 1980-2013. A random intersection associated with tree nested in plot and a first-order autocorrelation structure was included in the models. We used an exponential variance structure in growth models since the residual spread enlarged at increasing cambial age (Zuur et al. 2009). Variables were standardized to enable direct comparison of predictors' coefficients. We calculated variance inflation factors (VIF) of the models containing all explanatory variables to assess collinearity among explanatory variables. VIF values larger than 2.5 indicate high collinearity among variables (Dormann et al. 2013). Since saturated models presented high collinearity between C_a and cambial age, sequential regression was used to create a new variable: "ageRes", which resulted from residuals obtained by fitting linear models of cambial age as a function of C_a (Graham 2003). The C_a was used as the main explanatory variable as ontogenic processes are known to be minor when compared with long-term effects of changes in C_a and climate (McCarrol & Loader 2004). Additional LMMs were fitted to evaluate the impact of iWUE on growth, in which fixed factors were iWUE, site, C_a, ageRes and their interactions.

The response of beech trees born before and after 1950 at the Mediterranean site was also assessed with LMMs. Fixed effects were seasonal temperature and water balance, age group, iWUE (only in growth models), and C_a. A random intercept to account for correlation within tree, a first-order autocorrelation structure and an exponential variance structure associated with cambial age (only in growth models) were also included in the models.

Random, temporal autocorrelation and variance structures were determined by comparing nested models, with and without the aforementioned structures, with the likelihood ratio test using the restricted maximum likelihood estimation procedure (Zuur et al. 2009). Fixed effects selection was based on the Akaike Information Criterion corrected for small sample size (AICc), and the models with the lowest AICc were selected, i.e. those most parsimonious (Burnham & Anderson 2002). We considered the models with substantial support to be those in which the difference in AICc was smaller than 2. The goodness-of-fit of selected models was evaluated with the pseudo-R^2 proposed by Nakagawa & Schielzeth (2013), which comprises marginal (R^2m) and conditional (R^2c) R^2 values. The R^2m accounts for the proportion of variance explained by the fixed effects, and the R^2c accounts for the proportion of variance explained by the whole model, i.e. fixed plus random effects. All statistical analyses were carried out with R version 3.1.3 (R Core Team 2014). Correlations between the mean

$\delta^{13}C$ series were calculated using *dplR* package (Bunn et al. 2016) and LMMs and model selection were conducted using *nlme* (Pinheiro et al. 2015) and *MuMIn* (Barton 2015) packages, respectively.

3. RESULTS

3.1. Growth patterns

Scots pine showed an increase in basal area increment (BAI) corresponding to the juvenile phase during the 1960s and early 1970s until the early 1980s when BAI stabilized at values of ~10 cm^2 $year^{-1}$ at both sites (Fig. 1). The beech population at the Mediterranean site reached an overall steady growth rate during the 1970s (BAI ~ 7 cm^2 $year^{-1}$). Note that a growth release was detected at this site during the late 2000s, which may be related to pine mortality due to strong wind events that enhanced beech BAI. At the continental site, beech individuals were younger and BAI stabilized in the early 1990s resulting in mean BAI values of *ca.* 15 cm^2 $year^{-1}$ during the 2000s (Fig. 1).

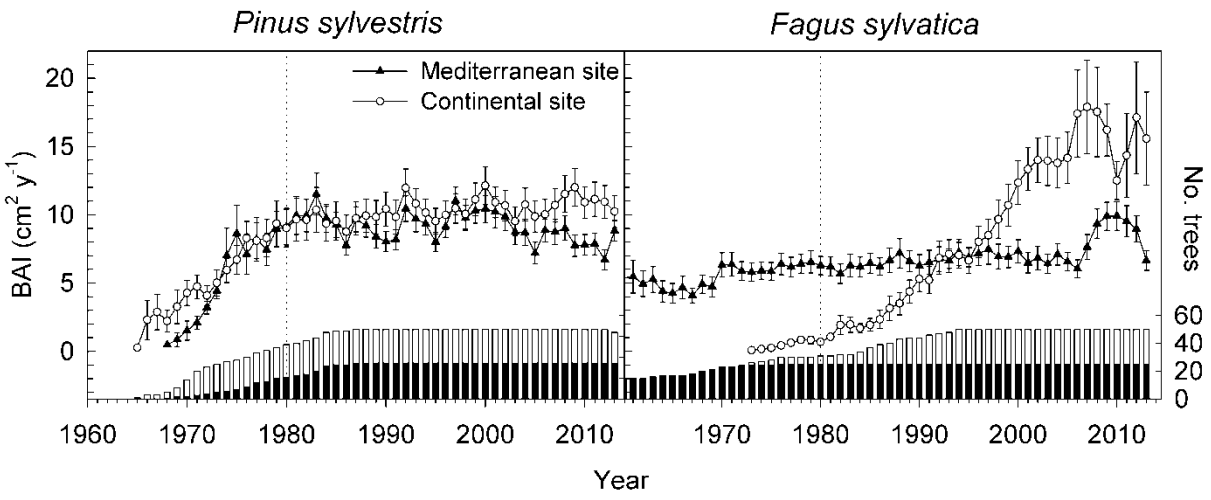

Figure 1. Annual basal area increment (BAI) of the two study species: Scots pine (*Pinus sylvestris*, left plot) and beech (*Fagus sylvatica*, right) in the two study sites. The bottom bars represent the number of radii measured every year. Error bars correspond to SEs. The dashed vertical lines indicate the start of $\delta^{13}C$ wood and iWUE data.

3.2. Isotope data

$\delta^{13}C$ showed a significant decreasing trend for both Scots pine ($P < 0.001$) and beech ($P = 0.006$) populations and it was significantly higher ($P < 0.001$) in the case of pine (-25.6‰) than in beech (-27.2‰). Trends did not differ between sites for pine ($P = 0.245$) or for beech ($P = 0.569$) (Fig. 2A). The correlations between the mean $\delta^{13}C$ series were stronger between Mediterranean and continental Scots pine populations ($r = 0.465$, $P = 0.112$) than between beech populations ($r = 0.411$, $P = 0.077$).

Scots pine reached higher mean iWUE values (92.93 ± 0.44 µmol mol^{-1}, mean ± SE) than beech (80.19 ± 0.60 µmol mol^{-1}). Both species significantly increased ($P < 0.001$) their iWUE since 1980,

although beech experienced an increase (+21.9 %) significantly greater ($P < 0.001$) than Scots pine (+12.2 %). There were no significant differences between populations in the rate of change of iWUE for pine ($P = 0.236$) or for beech ($P = 0.585$). However, the increasing tendency was consistently higher at the Mediterranean site (+16.8 % pine and +28.2 % beech) than at the continental site (+7.6 % pine and +15.7 % beech) (Fig. 2B).

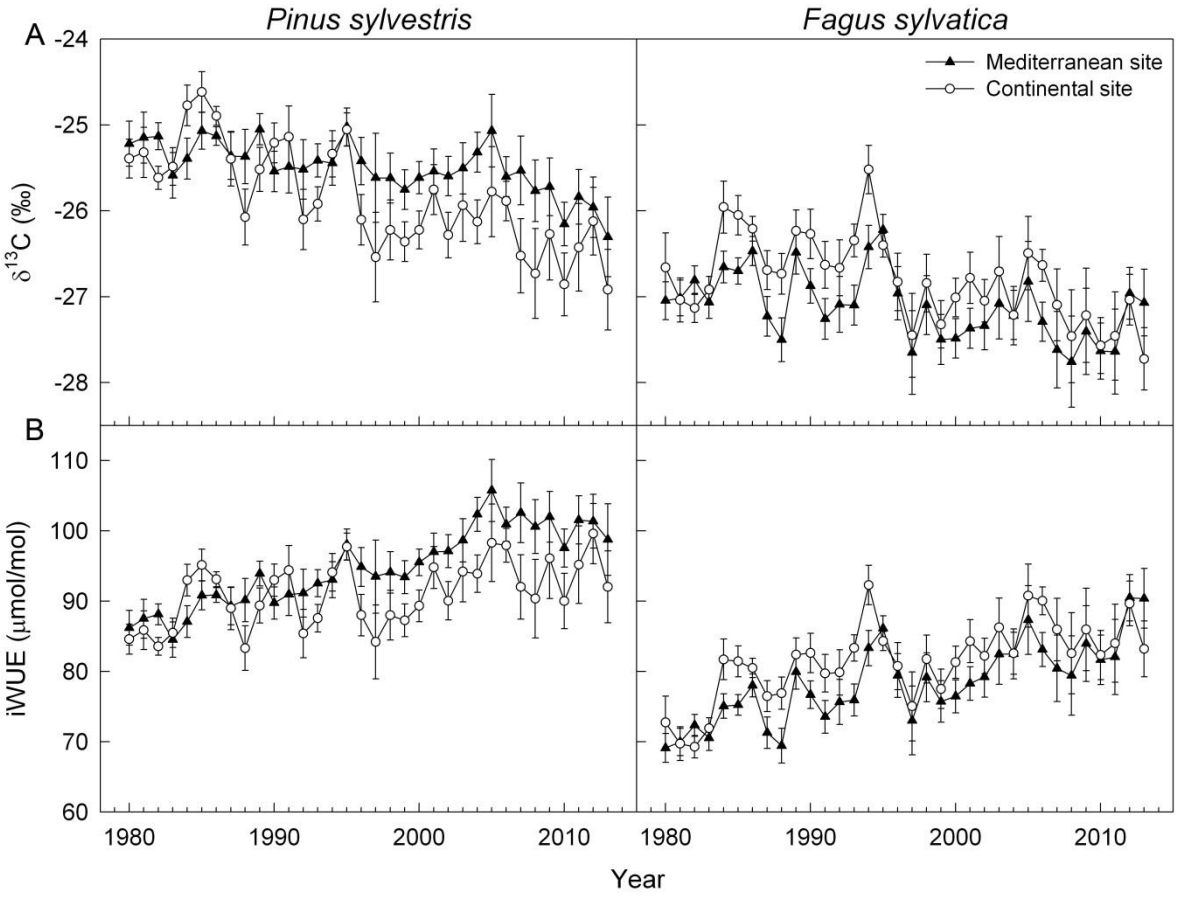

Figure 2. (A) Variations in carbon isotope ratio ($\delta^{13}C$) and(B) intrinsic water use-efficiency (iWUE) annual values of Scots pine (*Pinus sylvestris*, left) and European beech (*Fagus sylvatica*, right) in the two study sites. Error bars correspond to SEs.

3.3. Climate-growth-isotope associations

We found significant effects of climatic variables on both growth and iWUE trends. Mild temperatures during the early growing season (spring) enhanced beech growth, while pine growth was negatively affected by warm temperatures during the autumn prior to tree-ring formation.

Positive water balance during the growing season (spring and summer for Scots pine and only spring for beech) also improved growth. Water availability of the previous autumn also showed a positive effect on pine growth (Table 2). The drier summer conditions were, the greater the iWUE was. Warm summer temperatures also improved pine iWUE (Table 3).

Table 2. Parameter estimates for the selected linear mixed-effects models s fitted to explain changes in basal area increment (BAI) during the period 1980-2013. Bold values indicate effects significant at $P < 0.05$. Only those factors of the best model obtained by minimizing the Akaike´s information criterion (AIC) are shown.

Species	R^2m	R^2c	Fixed effects	
Scots pine (*Pinus sylvestris*)	0.190	0.681	T_{aut-1}	**-0.059**
			$P\text{-}PET_{aut-1}$	**0.032**
			$P\text{-}PET_{spr}$	**0.031**
			$P\text{-}PET_{sum}$	**0.056**
			site	-0.165
			C_a	0.010
			ageRes	**0.358**
			$DCI_{intra-sp}$	**-0.203**
			$DCI_{inter-sp}$	-0.020
			C_a x $DCI_{intra-sp}$	**0.067**
			site x $DCI_{inter-sp}$	**0.534**
European beech (*Fagus sylvatica*)	0.415	0.524	T_{spr}	**0.016**
			$P\text{-}PET_{spr}$	**0.022**
			site	**1.830**
			C_a	0.032
			ageRes	0.216
			$DCI_{intra-sp}$	-0.116
			C_a x site	**0.574**
			C_a x $DCI_{intra-sp}$	**-0.075**
			site x ageRes	**1.163**

Fixed effects were: seasonal temperature (T) and water balance (P-PET), site, atmospheric CO_2 concentration (C_a), derived variable from the cambial age of the tree-ring (ageRes), intra-specific degree of spatial-competition ($DCI_{intra-specific}$), and inter-specific degree of spatial-competition ($DCI_{inter-specific}$). In the case of climate variables, subscripts correspond to seasons and "-1" indicates the year prior to tree-ring formation.

R^2m and R^2c correspond to marginal (proportion of variance explained by the fixed factors) and conditional (proportion of variance explained by fixed plus random factors) R^2 values, respectively, calculated following Nakagawa & Schielzeth (2013). Random factors were the trees nested in plots sampled at each site, being the residual variance $\sigma^2 = 0.563$ and $\sigma^2 = 0.643$ for *P. sylvestris* and *F. sylvatica* models, respectively. A first-order autocorrelation structure and exponential variance structure associated with cambial age were also included in the models.

Table 3. Parameter estimates for the selected linear mixed-effects models fitted to explain changes in intrinsic water use-efficiency (iWUE) during the period 1980-2013. Bold values indicate effects significant at $P < 0.05$. Only those factors of the best model obtained by minimizing the Akaike´s information criterion (AIC) are shown.

Species	R^2m	R^2c	Fixed effects	
Scots pine (*Pinus sylvestris*)	0.454	0.707	T_{sum}	**0.064**

			P-PET$_{sum}$	**-0.190**
			C_a	**0.226**
			site	0.161
			DCI$_{intra-sp}$	**0.532**
			DCI$_{inter-sp}$	**0.998**
			site x DCI$_{inter-sp}$	**-0.816**
European beech (*Fagus sylvatica*)	0.346	0.541	P-PET$_{sum}$	**-0.208**
			C_a	**0.443**
			DCI$_{inter-sp}$	**-0.415**
			C_a x DCI$_{inter-sp}$	**0.145**

Fixed effects were: seasonal temperature (T) and water balance (P-PET), site, atmospheric CO_2 concentration (C_a), derived variable from the cambial age of the tree-ring (ageRes), intra-specific degree of spatial-competition (DCI$_{intra-specific}$), and inter-specific degree of spatial-competition (DCI$_{inter-specific}$). In the case of climate variables, subscripts correspond to seasons and "-1" indicates the year prior to tree-ring formation.

R^2m and R^2c correspond to marginal (proportion of variance explained by the fixed factors) and conditional (proportion of variance explained by fixed plus random factors) R^2 values, respectively, calculated following Nakagawa & Schielzeth (2013). Random factors were the trees nested in plots sampled at each site, being the residual variance σ^2 = 0.594 and σ^2 = 0.688 for *P. sylvestris* and *F. sylvatica* models, respectively. A first-order autocorrelation structure was also included in the models.

3.4. Competition and environmental influences on growth and carbon isotopes

The highest R^2 of regressions of mean tree iWUE as a function of the spatial competition index (*DCI*) was reached for neighbourhoods at distances around the focal tree of 9 m for Scots pine and 5 m for European beech, respectively (Fig. S3).

LMMs highlighted significant relationships among *DCI*, atmospheric CO_2 concentration (C_a) and BAI of Scots pine and beech (Table 2). Growth was reduced at high levels of intra-specific competition compared to low DCI_{intra} values. However, the intra-specific competition influence on growth evolved differently as C_a changed in each tree species: differences between competition levels declined for pine but rose for beech as C_a increased (Figs. 3A and 3B). Significant differences between beech populations were found for the relationship BAI-C_a, so that trees from the continental site presented positive and more pronounced response to rising C_a than trees from the Mediterranean site (Fig. S4). The impact of inter-specific competition on pine growth differed between sites: it had a positive impact at the continental site and negative at the Mediterranean site (Fig. 4A). As expected, C_a affected significantly and positively iWUE of both pine and beech. Scots pine presented higher iWUE under greater levels of both types of competition (Fig. 3C), although for inter-specific competition the trend was significant only at the Mediterranean site (Fig. 4B). Beech trees exposed to low inter-specific competition showed greater iWUE compared to those under high DCI_{inter} values, however the differences between inter-specific levels decreased as C_a rose (Table 3) (Fig. 3D).

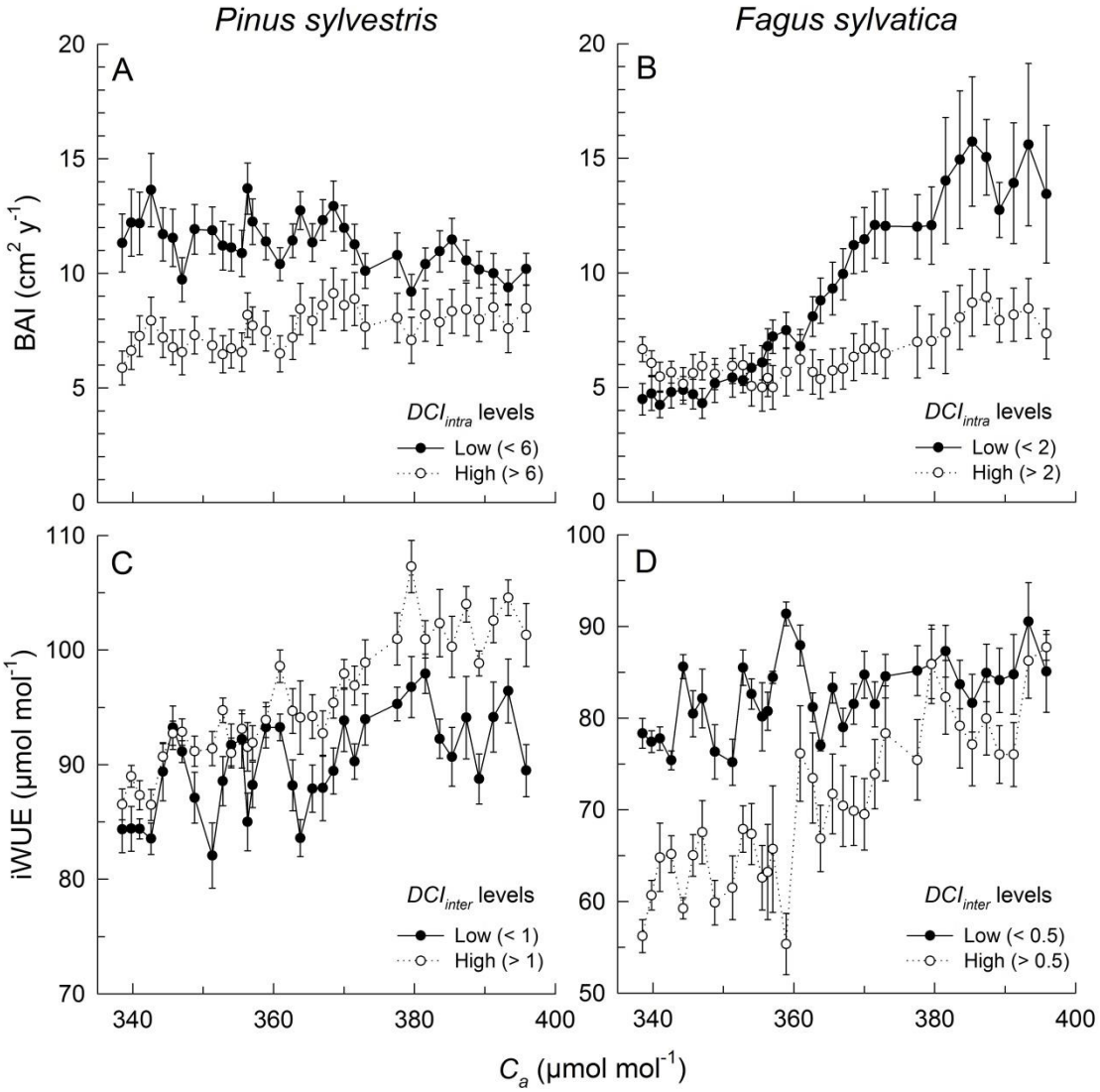

Figure 3. Variations in basal area increment (BAI) as a function of changes in atmospheric CO_2 concentrations (C_a) for low and high intra-specific competition levels for Scots pine (*Pinus sylvestris*, A), and European beech (*Fagus sylvatica*, B). The lower plots show changes of intrinsic water use-efficiency (iWUE) and C_a for low and high inter-specific competition levels of Scots pine (C), and beech (D). Each tree has been assigned to a competition level according to whether its competition status was below (low) or above (high) the average competition for the species.

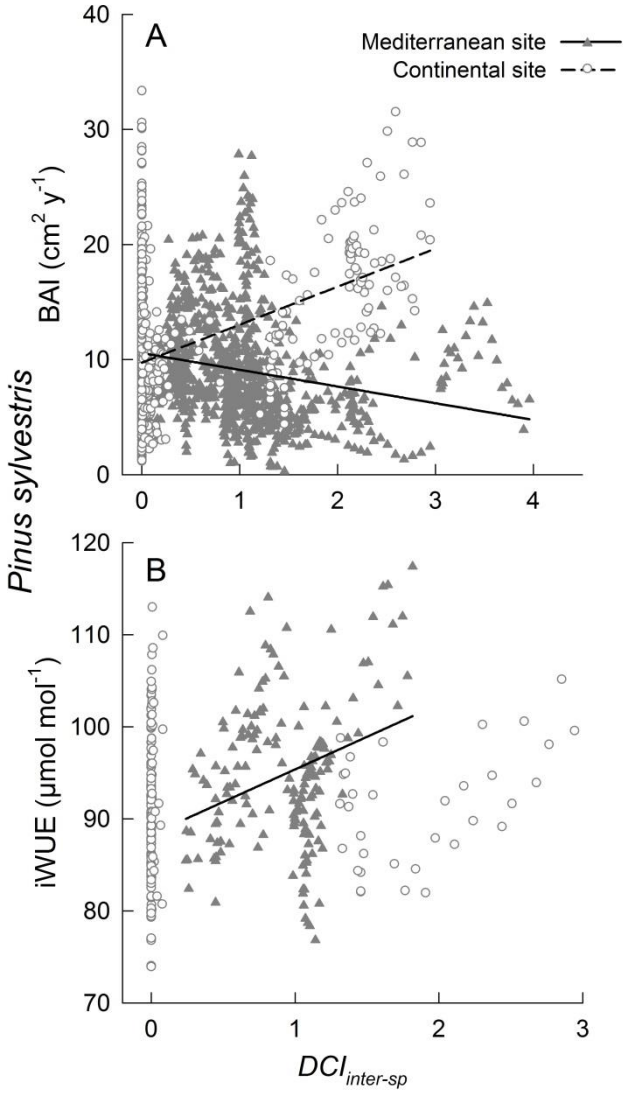

Figure 4. Site differences in the relationships found between inter-specific competition degree and basal area increment (BAI) (A) and intrinsic water use-efficiency (iWUE) (B) of Scots pine (*Pinus sylvestris*). Solid lines represent significant trends for the Mediterranean site data and dash lines represent significant trends for the cold-wet continental site data.

3.5. Ontogenetic changes in growth and carbon isotopes

Despite the fact that the sampled trees were young to mature (34-97 years old in beech and 37-74 years old in Scots pine), the iWUE of both species was not significantly affected by tree-ring cambial age (Table 3). Thus, a juvenile effect of tree-ring cambial age on iWUE values can be regarded as negligible. However, growth presented significant positive effects of cambial age (Table 2), probably because the study period included juvenile growth phases of some trees. In the case of beech populations, the rising BAI effect as a result of increasing cambial age differed between sites: the population in the continental site, which is younger, presented higher rates of growth (see Table 1).

The iWUE showed significant associations with growth of both species but of different signs. Negative BAI-iWUE relationships were found in the case of Scots pine ($P < 0.001$; Fig. 5A) without differences between sites, while positive BAI-iWUE associations were observed in beech (Fig. 5B), although only the Mediterranean population showed a significant relationship ($P < 0.001$).

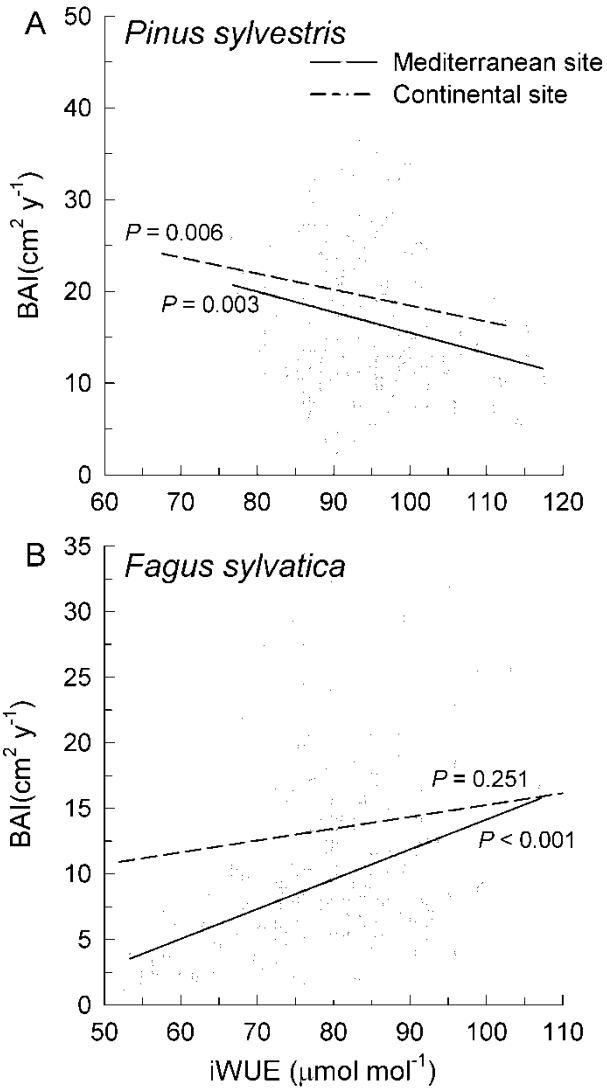

Figure 5. Relationships observed between intrinsic water use-efficiency (iWUE) and growth (basal area increment, BAI) in the two study sites for Scots pine (*Pinus sylvestris*, A), and European beech (*Fagus sylvatica*, B).

Finally, we analysed beech trees response in terms of BAI and iWUE at the Mediterranean site. Age group (two categories: born before and after 1950), C_a, as well as the interaction between them exerted an effect on both variables (Table S1). The higher C_a was, the greater the growth and iWUE were. However, trees born before 1950 had a more pronounced response to C_a increases than trees born during the second half of 20th century (Fig. S5). Beech iWUE was significantly associated to growth irrespective to the period of tree development (Table S1). Regarding climatic conditions, only summer water availability showed significant negative associations with iWUE.

4. DISCUSSION

The beneficial effects of admixing have been shown to provide an overall 25 % increase in productivity across forest types (Zhang et al. 2012) and a 12 % increase at European scale in Scots pine – European beech mixtures (Pretzsch et al. 2015). However, there is a scarcity of knowledge on what are the mechanisms that promote such complementarity effects leading to increased productivity in pine – beech mixtures despite their frequent occurrence and economic importance (Pretzsch et al. 2015). In this study we combined the analysis of intrinsic water use-efficiency (iWUE)

and basal area increment (BAI) trends to disentangle the species-specific responses to intra- and inter-specific competitive pressures and to long-term changes in atmospheric CO_2 concentration (C_a) and climatic conditions, focusing on the impacts of drought events on growth and iWUE. Our first hypothesis was supported only for Scots pine growth at the cold-wet continental site, since competition for water prevented any beneficial effect of the admixture of beech at the warm-dry Mediterranean site. The positive relationship found between BAI and iWUE for beech populations supports our second hypothesis. However, any advantage conferred by an increased iWUE did not compensate for other growth constraints in pine populations.

4.1. Species and site-specific growth sensitivity to climate and competition

Tree water status has been proposed to be a major limiting factor of radial growth for both Scots pine (Martínez-Vilalta et al. 2008, Primicia et al. 2013) and beech (Gutierrez 1988, Dittmar et al. 2003, Lebourgeois et al. 2005), in agreement with our results (Table 2). Drought constraint of growth is particularly important in the southernmost part of temperate species distributions (Linares & Camarero 2012). Soil water availability ought to be especially important in late spring and early summer, when the rate of wood production peaks (Rossi et al. 2009, Primicia et al. 2013). Additionally, water supply at the end of the growing season has been proposed to indirectly affect pine growth through an enhanced synthesis of carbohydrates, which are then mostly allocated for earlywood formation during the following year (Michelot et al. 2012).

Growth of the two studied species responded differently to seasonal temperatures (Table 2). Negative effects of high autumn temperatures on pine growth may be caused by an increase in atmospheric water demand that produced greater drought stress, as has been observed for other Scots pine populations in northern Spain (Martínez-Vilalta et al. 2008). This stress promoted a strong reduction in stomatal conductance (g), together with an enhancement of respiration rates and a decrease in stored carbon pools (Wullschleger et al. 2002). For beech, warm temperatures and the absence of frosts during spring could favour early season photosynthesis and trigger cambial reactivation thus increasing growth rate (Michelot et al. 2012). Rising temperatures during the growing season generally had a negative effect on conifer growth but positive on broadleaved species (Way & Oren 2010, Michelot et al. 2012, Coll et al. 2013). Several hypothesis have been proposed to explain this contrasting growth response, such as extended phenology (see Gómez-Aparicio et al. 2011), or differences in leaf traits (lifespan, mesophyll CO_2 conductance, photosynthetic capacity, stomatal density) resulting in significantly different physiological responses to environmental factors (Way & Oren 2010). Therefore, while a decrease in water availability will likely produce the same general reduction in growth of both species, a warmer climate would cause a performance disadvantage of pine compared to beech.

Nonetheless, tree growth is a multi-faceted biological process that can depend simultaneously on several interacting factors besides climate. In this study, site conditions and their interactions with biological variables, such as competition and tree age, outperformed climatic variables as tree growth drivers of both species (Table 2). Likewise, previous studies found tree growth and the effect of trees' interactions to be highly dependent on local environmental conditions across boreal, temperate and

Mediterranean forests (Gómez-Aparicio et al. 2011, Forrester et al. 2016, Madrigal-González et al. 2016). Resource availability and community structure are site-specific characteristics that may be critical for trees' function. The significant contribution of the random factors (tree and plot) in our LMMs, especially for pine growth, also pointed out that other site-specific drivers such as microclimatic or edaphic variations within sites and plots may affect the relationship tree growth – climate, competition and C_a.

Tree-to-tree competition has been shown to play a key role in tree sensitivity to environmental factors and in the resulting growth (Piutti & Cescatti 1997, Linares et al. 2010, Martín-Benito et al. 2010, Fernández-de-Uña et al. 2016). The differential effects of intra- and inter-specific competition are receiving increasing attention due to the encouragement for managing mixed forests (Messier et al. 2013). We found that intra-specific competition exerted negative influence on radial growth of both species (Fig. 3A and 3B), while inter-specific interactions enhanced growth in pine populations at the continental site and lessened it at the Mediterranean site (Fig. 4A).

Strong impact of intra-specific competition on pine growth (Fig. 4A) may be explained by the high susceptibility of this species to competition for light (e.g. Martín-Benito et al. 2010, Jucker et al. 2014). It agrees with the high mortality observed at the study area by Primicia et al. (2013, 2016). Besides, the fading of this effect as C_a rose might be explained by the reduction of the advantage conferred to less shaded trees as a consequence of the net rate of photosynthesis (A) enhancement resulting from increases in C_a. The admixture of beech likely benefited pine by opening gaps within pine stands, i.e. lessening self-shading. The different ecological traits and structural morphology of these two tree species can enhance stand structure heterogeneity resulting in canopy stratification and higher light interception and thus productivity (Pretzsch et al. 2016). Indeed, complementary traits regarding light use strategies have been proposed as mechanisms driving positive biodiversity-productivity relationships (e.g. Zhang et al. 2012, Forrester & Albrecht 2014, Forrester & Bauhus 2016).

However, tree species do not compete only for light but also for belowground resources. In this regard, our results suggest that light-related interactions can be overcome by competition for water in drought-prone environments if complementarity regarding water resources does not occur. Pretzsch et al. (2016) reported a positive relationship between water availability and vertical structuring in mixed stands of Scots pine and European beech at continental scale. Similarly, light absorption and light use-efficiency in mixtures have been shown to increase as climatic conditions improved (Forrester & Albretch 2014). However, Grossiord et al. (2014a) stated that drought resistance is enhanced in mixtures as long as net water-use partitioning or water related facilitation processes take place. Consistently with our results, a strong dependence of drought stress reduction on species identity and site conditions in mixtures has been reported from different regions in Europe (Forrester et al. 2016). This pattern is consistent with the 'complementarity – competition' framework proposed by Forrester & Bauhus (2016), since it predicts that species complementarity increases as water availability increases when interactions improve light absorption. In addition to water availability, nutrient cycling can also be affected by species mixtures (Blanco et al. 2017). European beech leaf litter has higher nutrient content, lower C/N ratio and less recalcitrant compounds

compared to Scots pine litter (Rothe & Binkley 2001, Pretzsch et al. 2015). Hence, the input of beech litter may have improved nutrient availability and allowed pine trees to develop bigger crowns.

The Mediterranean site is characterized by summer water deficit that combined with faster depletion of soil water and higher canopy rainfall interception in mixtures compared to pure pine stands (Primicia 2012, Grossiord et al. 2014b), may have led to strong inter-specific competition for water resources. Larger pine stem sizes at this site could also increase their vulnerability to drought (Table 1; Hember et al. 2016). Supporting our results, Primicia *et al.* (2013, 2016) found a reduction in pine radial growth due to beech presence modulated by stand density at the same site. Therefore, such water-related competition would have cancelled the light-related complementarity effects. The trade-offs between shade and drought tolerance (due to contrasting structural and physiological adaptations required to face scarcity of each resource) has been supported by eco-physiological studies (reviewed in Holmgren et al. 2012).

On the other hand, we observed a significant effect of intra-specific competition on beech growth (Fig. 3B), agreeing with the low self-tolerance previously suggested for this species (e.g. Río et al. 2014). Contrary to the pine, differences between high and low competition levels grew bigger as C_a increased. Higher C_a would have boosted A, thus increasing the demand for limiting belowground resources, especially water. Thus negative effects of competition may have increased faster in denser stands (Sohn et al. 2016). Regarding inter-specific competition, the lack of growth response to pine admixture is likely explained by the ability of beech to tolerate shade, as has been proposed for other *Fagaceae* species (i.e. oak) when mixed with pine species (Coll et al. 2013, Jucker et al. 2014). Besides, beech may have overcome pine when competing for above and belowground resources as a result of its highly efficient use of growing space (Dieler & Preztsch 2013) and highly competitive root system (Curt & Prévosto 2003).

4.2. Contrasting responses of iWUE to competition

The observed increase of iWUE of both pine and beech during the last decades (Fig. 2B) has been also described for different tree species and across diverse biomes (e.g. Peñuelas et al. 2011, and references therein). The observed iWUE changes laid in the same range previously reported for pine species (Andreu et al. 2008, Andreu-Hayles et al. 2011, Granda et al. 2014) and beech (Duquesnay et al. 1998, Peñuelas et al. 2008). This increase is mainly explained by the sharp rise in intercellular CO_2 concentration (C_i) because of the rise of C_a (+16.9 % since 1980) (see coefficients in Table 3), which probably increased carbon assimilation or reduced water loss by transpiration (Waterhouse et al. 2004, Huang et al. 2007).

Even though increased C_a accounted for a high variation of the iWUE, there might be other environmental factors modulating the responses (Peñuelas et al. 2011). We found an enhancement of iWUE when water shortage and high temperatures during summer occurred, and such enhancement was greater at the drought-prone Mediterranean site for both species (Table 3). iWUE has been shown to increase in response to the effect of a decrease in either air humidity or soil moisture (Wullschleger et al. 2002, Waterhouse et al. 2004, Linares & Camarero 2012). At the leaf level, trees under drought conditions have to manage the trade-off between optimum carbon gain for growth and loss of water

through transpiration (Farquhar et al. 1982), which results in a reduction in *g* and thus an increase in iWUE (see equation 3). Although iWUE was higher for Scots pine (likely due to a better stomatal control of water losses than beech, Madrigal-González & Zavala 2014), the magnitude of increase over time was lower (ca. +12 %) compared with that of beech (ca. +22 %). The stronger iWUE response of beech may be the result of the particularly drought-sensitive nature of this species (Waterhouse et al. 2004, Lebourgeois et al. 2005). Further, an age effect was not found in the iWUE response of any species, while growth was enhanced at increasing cambial age of tree-rings. Andreu et al. (2008) suggested that higher impacts of local and ontogenetic factors may be mirrored in radial growth and C stable isotopes might be more affected by climatic signals, which could explain the observed age effect pattern.

Stand structure exerted greater impact on iWUE patterns than climate, as observed with radial growth (Table 3). Previous studies have showed a variety of physiological responses to competition including increasing, decreasing or non-significant trends (McDowell et al. 2006, Linares et al. 2009, Martín-Benito et al. 2010, Metz et al. 2016). For our research sites, a contrasting response of iWUE of each species at increasing inter-specific competition was found: positive relationship for pine and negative for beech (Figs 3C and 3D). Differences in iWUE changes can result from variations in *A*, *g* or the ratio between them as a consequence of physical and biotic factors (Francey & Farquhar 1982).

In the case of Scots pine, both the reduction of self-shading mediated by beech and the enhancement of drought stress suffered by pine trees due to a strong competition for water resources (as supported by a significant impact of inter-specific competition only found at the Mediterranean site; Fig. 4B) could cause increases in *A* and reductions of *g*, respectively, and thus iWUE improvement at rising inter-specific competition levels. On the other hand, pine admixture could release beech's intra-specific competition for water and increase soil water availability through lower transpiration rates and canopy interception (González de Andrés et al. 2017). As a consequence, a reduction in water stress may have enhanced *g* and thus reduced iWUE. In addition, beech trees subjected to low inter-specific competition levels might have received higher radiation and then displayed greater *A* and iWUE (Linares et al. 2009). This explanation is supported by the small spatial scale (6 m) at which competing neighbours influenced beech iWUE (Fig. S3), and the fading of the competition effect as beech trees reached the canopy (Fig. 3D). The contribution of each process cannot be resolved from our data since knowledge of the combined use of carbon and oxygen isotopes ratios would be required (Scheidegger et al. 2000). However, these results are consistent with those from Fernández-de-Uña et al. (2016), who suggested that competition may modulate iWUE response as long as water, nutrients or light availability are limiting.

4.3. Growth-iWUE relationship differ between tree species

Regardless of the iWUE improvement observed in Scots pine since 1980, stem radial growth enhancement was not observed (Fig. 5A). The uncoupling between iWUE and growth is evident for both populations of Scots pine. This phenomenon has been reported for other tree species, biomes and regions (e.g. Silva et al. 2010, Peñuelas et al. 2011), including other pine species from Mediterranean, continental and high-elevation areas situated in the Iberian Peninsula (Andreu-Hayles et al. 2011,

Granda et al. 2014). On the contrary, Martínez-Vilalta et al. (2008) found an overall increase in Scots pine radial growth in NE Spain during the 20th century, which they attributed to rising C_a and increase in nutrient availability. Therefore, a combination of climatic and non-climatic environmental stresses may explain our results. Drought stress could override the beneficial effects of rising C_a and enhanced iWUE in terms of radial growth if water availability is not enough to maintain the demand of higher priority organs (fine roots or foliage) rather than the xylem (Brueggemann et al. 2011, Lévesque et al. 2014). Further pine photosynthetic capacity was likely limited by nutrients at the study sites (Blanco et al. 2008, 2009). Indeed, nutrient limitation has also been shown as an important factor preventing any CO_2 fertilization effect (Francey & Farquhar 1982, Silva et al. 2010).

As for European beech, our results suggest a positive growth trend at increasing iWUE, and a positive iWUE – growth association, particularly strong at the Mediterranean site (Fig. 5B). Similarly, Tegel et al. (2014) found growth increase in beech populations from the Balkan Peninsula (i.e. south-eastern edge of the species distribution) despite drier conditions. These findings contrast with climate-related growth declines previously reported in several studies focused on low-altitude populations at the southern range-edge of this species in Europe (Piovesan et al. 2005, Peñuelas et al. 2008). The enhancement of A due to a higher incident radiation as beech approached and reached the pine canopy may have enhanced not only iWUE but stem radial growth as well. However, such size-related effects do not explain this outcome because the relationship should be stronger at the continental site where water shortage is lower, an effect not noticed during our research.

A slower rate of soil water depletion as a result of the increase in iWUE, and thus reduced transpiration may increase the advantage of trees growing in drought-prone environments. In fact, changes in soil moisture induced by rising C_a have been proposed to be a major component of the CO_2 fertilization effect (Morgan et al. 2007). For instance, improved growth due to improved iWUE, especially in dry sites, was found in ponderosa pine forests (Soulé & Knapp 2006). However, growth decline was also reported for the same species (Lévesque et al. 2014). Warmer and longer growing seasons could also stimulate growth (Martínez-Vilalta et al. 2008). Additionally, the higher plastic nature of beech leaves (Forey et al. 2016) and vessel traits (Diaconu et al. 2016), among other characteristics, compared to pine (Pretzsch et al. 2016) could promote a better physiological adjustment of beech trees under long-term environmental changes.

Thus, beech trees experienced a potential CO_2-fertilization effect even though there was a decrease in water availability. Nonetheless, we observed a progressive uncoupling between beech´s growth, iWUE and rising C_a (Table S1; Fig. S5). Similar declining responses have been reported in other studies for beech (Peñuelas et al. 2008), and for other tree species (Waterhouse et al. 2004, Linares et al. 2009, Linares & Camarero 2012). Several explanations have been proposed for decreasing sensitivity of iWUE to C_a, such as a threshold in low water availability that limits the iWUE improvement (Peñuelas et al. 2008, Linares et al. 2009), or long-term anatomical and physiological adaptations for adjusting C_i to increasing C_a such as changing stomatal density or A (Ward et al. 2005). The rise in C_a may not compensate the reduction in water availability, explaining the reduced growth response to rising C_a as has been suggested for several Iberian forests (e.g. Peñuelas et al. 2008, Camarero et al. 2015). Additionally, forest densification due to increased abandonment of both

agricultural fields and forest management practices over the last decades could have led to competition intensification in extensive areas of mountainous Spanish forests (e.g. Coll et al. 2013). Such competition intensification may have played an important role reducing both iWUE and growth of beech trees born after 1950 (see sections 4.1 and 4.2).

5. CONCLUSIONS

In summary, Scots pine and European beech show contrasting responses to changes in climate and rising C_a, depending on their physiological strategies to face increasing water stress. Additionally, tree species responses to these global change components may be also modulated by local factors, such as nutrient availability (Blanco et al. 2017). Species complementarity was only found in Scots pine populations at the moistest site, suggesting a trade-off between drought and shade tolerance. Regarding iWUE, both species responded differently to inter-specific competition, with the response being positive for Scots pine but negative for European beech. The combined effect of competition and resource limitation could cause changes in photosynthetic rates and stomatal conductance and modulate iWUE, although the contribution of both processes cannot be disentangled with certainty. Therefore, tree-to-tree competition should be taken into account when designing management plans that improve forests' adaptation to climate change, as it has been shown to exert a varying influence on species performance.

Variations of mixing effects with ontogeny may also result from changes in light and soil resources availabily as stands develop (Forrester 2014). Thus, assessments of species interactions at longer time scales covering whole stand development may provide insight into mixtures functioning. However, there is scarcity or lack of long-term field studies on mixed-species forests. Besides, the predicted shift in environmental conditions hinders to obtain transferable conclusions to future forests from studies conducted under past conditions. Therefore, modelling approaches may be of special interest in order to improve the understanding of long-term dynamics of mixed-species forests. In addition, some forest growth models allow to simulate projected changes in climatic conditions and nutrient inputs to the ecosystem (Blanco et al. 2015), and easily create virtual experiments where it is easier to monitor soil moisture and nutrient availability without the confounding effect of site-specific factors. These questions are the objectives of Chapter 2.

A review of the literature highlights the variety of radial growth responses to iWUE increases between and within species. Hence the influence of water use on growth processes depends on species features and climatic and site conditions. In our study, BAI-iWUE relationships were negative for Scots pine and positive for European beech. These contrasting behaviours have got implications for coping with the predicted increasing drought events of Scots pine-European beech mixtures located near the ecological limit of the two species. Furthermore, if the long-term CO_2 fertilization effect on forests is absent or undetectable (Scots pine) or declining (European beech) at broad continental scales as it is for the local scale tested in this work, the capacity of mixed conifer-broadleaf forests for carbon uptake and storage in the future could have been overestimated.

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CHAPTER 2

Increased complementarity in water-limited environments in Scots pine and European beech mixtures under climate change

Increased complementarity in water-limited environments in Scots pine and European beech mixtures under climate change

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ABSTRACT

Management of mixedwoods is advocated as an effective adaptation strategy to increase ecosystem resiliency in the context of climate change. While mixedwoods have been shown to have greater resource use efficiency relative to pure stands, considerable uncertainty remains with respect to the underlying ecological processes. We explored species interactions in Scots pine / European beech mixedwoods with the process-based model FORECAST Climate. The model was calibrated for two contrasting forests in the southwestern Pyrenees (northern Spain): a wet Mediterranean site at 625 m.a.s.l. and a continental site at 1335 m.a.s.l. Predicted mixedwood yield was higher than that for beech stands but lower than pine stands. When simulating climate change, mixedwood yield was reduced at the Mediterranean site (-33%) but increased at the continental site (+11%). Interaction effects were enhanced as stands developed. Complementarity dominated the Mediterranean stand but neutral or net competition dominated the continental stand, which had higher stand density and water availability. Reduced water demand and consumption, increased canopy interception, and improved water-use efficiency in mixtures compared to beech stands suggest a release of beech intra-specific competition. Beech also facilitated pine growth through better litter quality, non-symbiotic nitrogen fixation and above- and belowground stratification, leading to higher foliar nitrogen content and deeper canopies in pines. In conclusion, mixtures may improve water availability and use efficiency for beech and light interception for pine, the main limiting factors for each species, respectively. Encouraging pine-beech mixtures could be an effective adaptation to climate change in drought-prone sites in the Mediterranean region.

Keywords (8): Species complementarity, mixedwoods, ecological modelling, *Pinus sylvestris*, *Fagus sylvatica*, interspecific competition, intraspecific competition, Pyrenees.

1. INTRODUCTION

Climate is one of the main environmental factors determining forest ecosystems structure and function, as it affects key processes such as tree growth and mortality, nutrient cycling, and species interactions. Human-induced climate change is expected to result in escalating atmospheric and surface temperatures for the 21st century with associated changes in precipitation regimes and expected increases in the frequency and severity of extreme drought events in many parts of the world (IPCC 2013). It is anticipated that climate change will have both positive and negative impacts on forest growth depending on species characteristics and regional patterns. Expected positive impacts include increases in forest vigour and growth from improved water use efficiency associated with elevated atmospheric CO_2 concentrations, and longer growing seasons in temperature-limited ecosystems (Körner 2000, Huang et al. 2007). Expected negative impacts include growth reductions and mortality associated with increases in water and heat stress, and elevated mortality related to climate-driven changes in the dynamics of forest insects and pathogens (Allen et al. 2010).

The management of forests in a mixed condition (with two or more tree species) has been increasingly recognized as superior to monocultures with respect to the provision of a full range of ecosystem services (Loreau et al. 2001). Moreover, silviculture is gradually moving towards forest mixtures as an adaptation strategy designed to enhance ecosystem resiliency through the reduction of species-specific risks associated with global change (Jactel et al. 2009, Messier et al. 2013). The impacts of mixing species on stand-level productivity have been attributed to changes in nutrient and water availability, light-related interactions (light absorption and light use efficiency), and resilience to biotic or mechanical disturbances among others (Jactel et al. 2009, Richards et al. 2010, Forrester 2014, 2015). Such interactions between species tend to be dynamic in nature, changing along spatial and temporal gradients in resource availability and climatic conditions (Forrester 2014).

Inter-specific differences in physiology, phenology, or morphology can influence species and stand production (Forrester & Bauhus 2016). These processes are often grouped into the phenomena of facilitation (i.e. one species improves the resource availability, climatic or biotic conditions of another species) or competitive reduction (i.e. inter-specific competition in the mixture is lower than intra-specific competition in pure stands). However, the inter-dependence among ecological processes in mixtures makes it extremely difficult to separate the effects of facilitation and competitive reduction (Kelty & Cameron 1995, Loreau & Hector 2001, Forrester 2014). Alternatively, facilitation and competitive reduction have been described collectively as complementarity (Loreau & Hector 2001). Recent experimental studies (Forrester 2015), reviews (Forrester 2014, Forrester & Bauhus 2016) and modelling approaches (Wu et al. 2015, Forrester & Tang 2016) have analyzed such complementarity concept in forest ecosystems.

In Europe, the light-demanding Scots pine (*Pinus sylvestris* L.) and the shade-tolerant European beech (*Fagus sylvatica* L.) are the most widely distributed conifer and broadleaf species, and their distributions overlap over a large area of the continent (Fig.1). Although mixtures of beech and pine have been observed to provide an overall increase in yield of 12 % in comparison with pure stands (Pretzsch et al. 2015), it is unclear if this relationship will be consistent under different stand

conditions (e.g. ages, densities and edaphic conditions) and under changing climate conditions. As the climate in continental Europe shifts towards warmer and drier summers in the South, and warmer and wetter summers in the North (IPCC 2013), there is a potential for the range of Scots pine to expand northwards and upwards in elevation. In contrast, beech is expected to migrate towards higher elevations but to decline in lower and mid altitudes, where it could be replaced by pine or other species (Peñuelas & Boada, 2003). The Iberian Peninsula represents the southern and western limits of the range of both Scots pine and European beech (Fig. 1). Accordingly, this region is likely to be highly sensitive to climate change. Hence, an analysis of the potential impacts of climate changes on these rear-edge forests will provide valuable insight towards understanding long-term impacts of warmer and/or drier conditions throughout the broader range of these species.

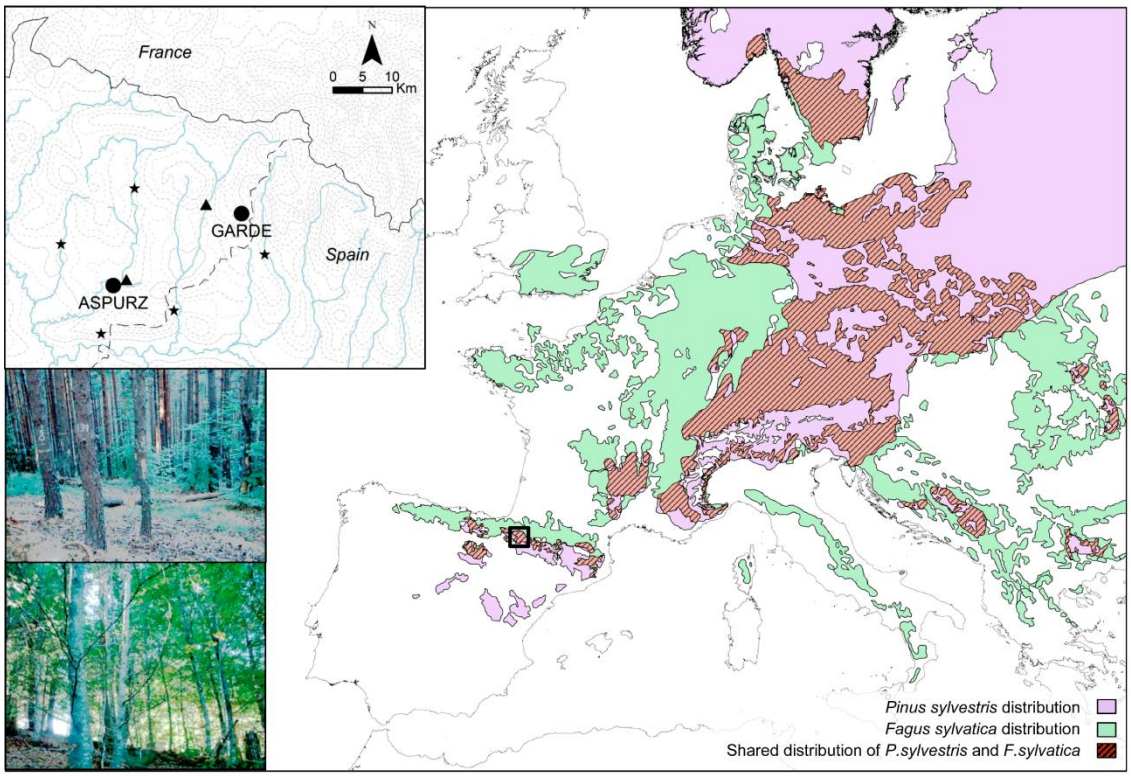

Figure 1. Natural European distribution of Pinus sylvestris, Fagus sylvatica (EUFORGEN, 2009) and the common area between both species. The left upper inset shows the location of experimental plots (circles): Mediterranean site (Aspurz) and continental site (Garde); weather stations providing historical climate (triangles) and weather stations averaged for climate change scenarios projection (stars). Lower pictures show images from experimental pine (upper) and beech (lower) stands.

Given the lack of long-term field studies in mixed forest and the uncertainty in changing climatic conditions, forest growth models provide one of the best available methods to examine long-term patterns of growth and development in mixedwoods and their potential behaviour under alternative climate change scenarios. Hybrid models combining ecological processes and empirical data can be

effective tools for projecting development under untested growing conditions, novel silvicultural regimes, and alternative species combinations and proportions (Blanco et al. 2015).

The objectives of this study are: 1) to explore underlying causes of complementarity and competition in mixed pine and beech forests in the southwestern Pyrenees, and 2) to evaluate the potential impacts of climate change on forest nutrient and water dynamics, and ultimately on tree growth and complementarity in two different study sites. Complementarity was considered to occur when the mixed stand growth exceeded from the weighted growth average of both pure stands (Loreau & Hector 2001). We hypothesize that pine and beech growing in intimate mixtures will experience improved water and nutrient availability, capture and/or use efficiency relative to pure stands, particularly under warmer and drier conditions associated with climate change. Likewise, we hypothesize that Iberian mixed pine-beech forests will be more productive than pure forests and that the complementarity effects will vary over time.

To test these hypotheses we have employed the process-based, ecosystem-level model FORECAST Climate (Seely et al. 2015) to simulate the development of forest ecosystems under a reference climate and different climate change scenarios derived from six global circulation models (GCMs) and two representative concentration pathways (RCPs). FORECAST Climate is able to simulate the movement of water through various forest layers including explicit representations of the balance between inputs from precipitation and seepage, and outputs by canopy interception, evapotranspiration, plant uptake, percolation and runoff. The model has been tested and applied for a wide variety of forest ecosystems (Dordel et al. 2011, Blanco et al. 2015, Lo et al. 2015, Seely et al. 2015, and references therein).

2. MATERIAL AND METHODS

2.1. Study sites

The study area is located in the southwestern Pyrenees in the province of Navarre (northern Spain; Fig.1). Using data from experimental plots monitored since 1999 (pine stands) and 2013 (beech stands), FORECAST Climate was calibrated to simulate two contrasting pine-beech mixedwoods: a Mediterranean low-elevation site (Aspurz), and a continental high-elevation site (Garde) (Fig.1, Table 1). In this region, management plans have favored the presence of pure stands of Scots pine, which is a more marketable species. However, more recently mixed stands have been encouraged by facilitating beech regeneration and growth under maturing pine canopies (Condés et al. 2013).

Table 1. Site characteristics (mean ± standard error) in 2014. Stands descriptors from Puertas (2001) and Iriarte and Puertas (2003).

Site	**Mediterranean site**		**Continental site**	
Name of the closest town	Aspurz		Garde	
Latitude	42º48'50'' N		42º42'31'' N	
Longitude	52'30'' W		1º8'40'' W	
Altitude (m.a.s.l.)	625		1335	
F.A.O. soil type	Haplic Alisol		Dystric Cambisol	
Climate type (Papadakis, 1970)	Cold wet Mediterranean		Cold wet continental	
	Pine stands	**Beech stands**	**Pine stands**	**Beech stands**
Slope (%)	7	37	40	45
Other overstory tree species [a, b]	*Fagus sylvatica* L. *Quercus humilis* L.	*Pinus sylvestris* L. *Alnus glutinosa* (L.) Gaertn	*Fagus sylvatica* L.	*Pinus sylvestris* L.
Site Index at stand age 80 years (m)	29	21	23	18
Age (years)	47	72	51	38
Density (stems ha^{-1}) [c]	1456 ± 140	700 ± 115	2747 ± 328	783 ± 118
Dominant height (m) [d]	20.4 ± 0.3	17.3 ± 0.8	17.3 ± 0.9	13.2 ± 0.5
Mean DBH (cm) [e]	18.9 ± 1.0	14.2 ± 0.7	14.8 ± 0.2	9.5 ± 0.4
Basal area (m^2 ha^{-1})	41.2 ± 0.9	13.5 ± 6.6	47.8 ± 1.6	15.0 ± 4.0

[a] Scots pine plots: eighteen and ten tree species identified in the Mediterranean and the continental sites, respectively
[b] European beech plots: seven and two tree species identified in the Mediterranean and the continental sites, respectively
[c] Trees with a diameter > 7.5 cm at breast height (1.30 m, DBH).
[d] Measured averaging (n = 100) the height of the thickest dominant trees per hectare.
[e] Measured by double cross measurement.

Historical climate data were obtained from the nearest weather stations to each study site. Due to the elevation difference between the continental experimental plots and the closest weather station (about 600 m), climate data were adjusted using the MounTain microCLIMate simulation model (MT-CLIM; Running et al. 1987). Maximum and minimum temperature lapse rates and precipitation isohyets needed for the extrapolation were calculated from regional climate data. Missing data were calculated by interpolating values from nearby weather stations. For the period 1975-2004 mean growing season (May-October) temperature was 16.8 ºC and 14.5 ºC and precipitation amount was 402 mm and 743 mm for the Mediterranean and continental sites, respectively (Fig. 2). Summer droughts are frequent in the Mediterranean site. Soil characteristics are summarized in Table 2.

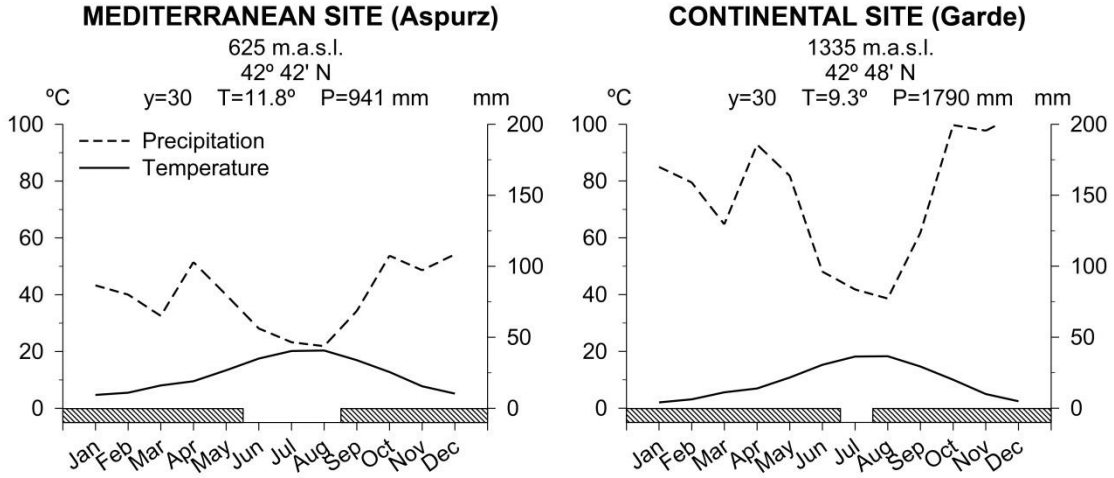

Figure 2. Climatic diagrams for the study sites for the period 1975-2004 for the Mediterranean site (Aspurz) and the continental site (Garde). y represents number of years considered; T: mean annual temperature (ºC); P: mean annual amount of precipitation (mm). Oblique striped area shows months with an absolute minimum temperature below 0 °C.

2.2. Model description

FORECAST Climate is an ecosystem-level, non-spatial, stand-scale, forest growth simulator. It includes the basic FORest and Environmental Change ASsessment Tool (FORECAST; Kimmins et al. 1999) and the new hydrological module based on the Forest Water Dynamics model (ForWaDy; Seely et al. 1997). As the model has been recently described in detail (Seely et al. 2015), only a basic description is provided here. Basic FORECAST and FORECAST Climate versions have been validated in a wide range of forest types covering six different biomes (see Table S2), and thus showing a good portability. In addition, several sensitivity analyses have been conducted regarding carbon and nitrogen pools, stand density, mixing ratios of species, root biomass and decomposition, among others (Table S3). Hence, the model is considered to be sensitive but also robust against extreme values to key parameters of mixed-species forests.

2.2.1. The forest growth model FORECAST

The FORECAST model was designed to accommodate a wide variety of harvesting and silvicultural systems in order to compare and contrast their effect upon forest productivity, stand dynamics and a series of biophysical indicators of non-timber values. Tree growth is limited by available light and nutrients (Fig. S1A) and the model uses a mass balance approach to simulate nutrient cycling. Rates of key ecosystem processes are calculated at an annual time step from a combination of historical bioassay data (biomass accumulation in component pools, stand density, etc.) and measures of certain ecosystem variables (e.g., decomposition rates, photosynthetic saturation curves) by relating ''biologically active'' biomass components (foliage and small roots) with calculations of nutrient uptake, the capture of light energy, and net primary production. In this way the model generates a set of growth properties for each tree and plant species which includes, among others, 1) photosynthetic efficiency per unit of foliage biomass based on relationships between foliage biomass, simulated self-shading, and net primary productivity after accounting for litterfall and mortality, 2) nutrient uptake requirements based on rates of biomass accumulation and nutrient concentrations in different biomass components on different site qualities, and 3) light-related measures of tree and branch mortality derived from stand density input data in combination with simulated light profiles. The model simulates the dynamics of all major forest carbon stocks (aboveground biomass, belowground biomass, litter, dead wood and soil organic carbon). It complies with the carbon estimation methods outlined by the IPCC (IPCC 2013). See the Appendix B and Kimmins et al. (1999) for further details.

2.2.2. The forest hydrology model ForWaDy

ForWaDy (Seely et al. 1997) is a two-dimensional forest hydrology model that simulates the hydrological dynamics of a forest stand on a daily time step under a given set of climatic and vegetation conditions. It has been validated against field-measured soil moisture data (Titus et al. 2006, Dordel et al. 2011). In the FORECAST Climate model, ForWaDy is dynamically linked to FORECAST to facilitate an explicit representation of water availability and competition for limited water resources on tree growth and other ecosystem-level processes. Reconciliation between the different temporal resolutions of each model is made through the usage of annual indices (calculated from the daily ForWaDy output) as input to FORECAST (Seely et al. 2015). Conversely, FORECAST provides annually updated input to ForWaDy in the form of species-specific estimates of leaf area index, canopy radiation interception, and soil occupation by fine root biomass. It also provides information regarding the formation of soil organic matter and its distribution within specific soil layers.

ForWaDy calculates potential evapotranspiration (PET) using net shortwave solar radiation interception and an empirically based energy budget approach. PET is estimated separately for the canopy, understory, and forest floor. Hydrological dynamics in the forest floor and rooting zone are simulated using a multi-layered approach (Fig. S1B). Water storage and vertical movement through each soil layer are regulated by its physical properties that dictate moisture holding capacity, permanent wilting point moisture content, and infiltration rate. Water stress is calculated daily for each species separately as the relative difference between potential energy-limited transpiration

demand and actual transpiration. This is represented by a dimensionless transpiration deficit index (TDI; Eq. 1):

$$TDI = \frac{CanT_{Demand\ i,d} - CanT_{Actual\ i,d}}{CanT_{Demand\ i,d}} \quad \text{(Eq. 1)}$$

where, CanTDemand, i,d is the energy-limited transpiration for species *i* on a day *d*, depending on leaf area index (LAI), intercepted short-wave radiation, canopy albedo, and canopy resistance; and CanTActual, i,d is the soil-limited transpiration, calculated as a function of CanTDemand, i,d, root occupancy, and available soil moisture. A higher TDI value indicates greater moisture stress. A detailed description of the ForWaDy model is presented in Seely et al. (1997, 2015).

2.2.3. Climate impacts on productivity, decomposition, and mortality

The impact of temperature and water availability on plant growth is represented in FORECAST Climate with species-specific curvilinear response functions (Fig. S2). A daily growth response index is calculated as the product of the temperature and moisture effects and summed over the year to generate an annual growth response index. A similar approach is utilized to represent the impact of temperature and moisture content on decomposition rates. Reference values for the annual climate response indices are determined from a series of climate calibration runs in which historical climate data from a 20 to 30 year reference period are used as model inputs. During climate change simulations, current-year climate response indices are compared against mean reference values to determine the degree to which species-specific base growth rates and litter-type specific base decomposition rates should be adjusted to account for climate effects. FORECAST Climate also includes a representation drought mortality associated with prolonged periods of water stress (Allen et al. 2010). Water stress mortality is simulated as a function of two-year running average water stress based upon TDI (Fig. S3). Further explanations are provided in the Appendix B.

2.3. Model calibration and simulation

2.3.1. FORECAST Climate calibration

Calibration data from Scots pine and European beech sites used to parameterize the base FORECAST model are provided in the Appendix B (Tables S2 and S3). In addition, the forest hydrology sub-model ForWaDy requires data describing characteristics of the soil profile from each site. These data were obtained by digging soil pits in each site (Table 2). Parameters regulating hydrological processes such as transpiration rates, soil water uptake and water stress development for simulated tree and plant species are provided in Table 3. A detailed summary of empirical and literature sources for model calibration data and input parameters is provided in the Appendix B.

Table 2. Soil chemical and physical properties in the study sites. Parameters in bold are plant-available water related values used to calibrate the hydrological submodel.

Site/Horizon	Texture	Coarse fragment content (%)	Depth [a] (cm)	pH 1:2.5 H_2O	Density [b] ($g.cm^{-3}$)	CEC ($cmol+.kg^{-1}$)	O.M. (%)	Soil C/N	Maximum field capacity (%)
Mediterranean site									
Horizon O	-	**0**	9.7	-	**0.24**	-	-	43.1	**32.0**
Horizon A	**Sandy loam**	**20**	**20.0**	6.25	0.38	18.6	10.41	23.3	**38.8**
Horizon B	**Sandy loam**	**20**	**50.0**	5.32	1.89	6.6	1.63	20.5	**38.8**
Continental site									
Horizon O	-	**0**	8.8	-	**0.24**	-	-	56.5	**32.0**
Horizon A	**Loam**	**30**	**25.0**	5.83	0.76	26.6	9.07	15.6	**38.8**
Horizon B	**Loam**	**30**	**60.0**	5.76	1.27	18.2	2.71	9.4	**38.8**

[a] The starting depth for the organic horizon (O) is shown as measure on the experimental sites, but it can change over time in the simulations depending on rates of litter production and decomposition.
[b] Organic horizon (O) density: estimated bulk density; mineral soil (horizons A and B) density: apparent density.

Table 3. Parameter values in the hydrological submodel specific to the simulation of evapotranspiration and water stress for trees and understory vegetation.

Species	**Canopy parameters**		**Permanent Wilting Point [d]**		**Maximum rooting depth (cm)**
	Albedo	Resistance[c]	Humus	Mineral soil (Med. / cont. sites)	
Pinus sylvestris [a]	0.09	0.2	0.13 / 0.13	0.10 / 0.15	40
Fagus sylvatica [a]	0.13	0.15	0.15 / 0.15	0.12 / 0.18	80
Rubus spp. [b]	0.12	0.15	0.12 / 0.12	0.13 / 0.13	25

[a] Tree species
[b] Understory species
[c] Reference relative canopy resistance to water loss through stomata. Higher values indicate greater resistance.
[d] Relative volumetric moisture content (proportion of total volume) at which soil water uptake is suspended.

2.3.2. Simulating climate change impacts on forest ecosystems

Performance of pure and mixed pine and beech forests in the southwestern Pyrenees under different climate change scenarios was assessed. Natural regeneration of both species was simulated as occurring at year 1 of simulation, with no further regeneration events. Seedling regeneration densities in the pure stands were based on regional growth and yield tables for these species (Madrigal et al. 1992, Puertas 2003). Condés et al. (2013) observed that stand density in Navarre's pine-beech mixedwoods is usually divided between pine and beech at 50%-50% species proportions. Similar average proportions were reported by Preztsch et al. (2015) for the whole natural range of both species across Europe. Therefore, seedling density for each species in mixed stands was set up as the 50 % of the density of each species in pure stands. This procedure allowed comparisons of species performance when growing alone and together with the other species. To obtain growth predictions meaningful for forests already established, climate change impacts were simulated starting on year 51, which was the average tree age in the experimental plots used to obtain empirical calibration values (see Table 1).

Three climate change scenarios were simulated: historical, moderate and severe. In the case of the historical scenario, atmospheric CO_2 concentration were held constant at 2004 levels (377 ppm) to approximate a no-change baseline. Historical climate data from the period of 1975-2004 (see section 2.1) were cycled five times to generate 150 years of daily data to represent the historical (no-change) climate scenario. The moderate and severe climate change scenarios were derived from six GCMs included as part of the Intergovernmental Panel on Climate Change AR5 analysis (IPCC 2013; Table S6). Two CO_2 emissions pathways that generate radiative forcing of 4.5 Wm^{-2} (RCP 4.5) and 8.5 Wm^{-2} (RCP 8.5) were selected, corresponding to moderate and severe scenarios, respectively (Meinshausen *et al.* 2011; Fig. S4). GCMs were downscaled using the Statistical Downscaling Model (SDSM; Wilby & Dawson 2013). The projections of five weather stations near the study sites (Fig. 1) were averaged to generate climate change scenarios. The resulting data sets spanned 100 years (2015–2114). Under these scenarios, mean growing season temperature in the Mediterranean and the continental study sites were predicted to rise from about 16.8 ºC and 14.2 ºC in 2015 to 19.7 ± 0.2 ºC and 15.2 ± 0.2 ºC (RCP 4.5) or 24.2 ± 0.4 ºC and 19.6 ± 0.4 ºC (RCP 8.5) by the beginning of the 22th century, respectively. However, there is a great variability among the precipitation predictions among models, and no common trends can be derived. Detailed descriptions of the modeled climate change scenarios are provided in the Appendix B (Figs. S5A and S5B).

2.4. Evaluation of stand-level performance through complementarity

Complementarity, which appears when the interactions between species have a net positive influence due to resource partitioning or facilitation (Loreau & Hector 2001), was assessed at species and stand levels with Eq. 2 and Eq. 3, respectively, at each time step (year) for each simulation conducted.

$$Species\ complementarity_{i,j}\ (\%) = 100\ \times \left(\frac{Y_{mixed\ i,j}}{Y_{mono\ i,j} \times Sp_{i,j}} - 1\right) \qquad \text{(Eq. 2)}$$

$$Mixed\ stand\ complementarity_j\ (\%) = 100 \times \left(\frac{Y_{mixed\ Ps,j} + Y_{mixed\ Fs,j}}{Y_{\ mono\ Ps,j} \times Sp_{Ps,j} + Y_{\ mono\ Fs,j} \times Sp_{Fs,j}} - 1 \right) \quad \text{(Eq. 3.)}$$

where *Ymixed i,j* is the stemwood yield of species *i* (Scots pine or European beech) in the mixed stand at year *j* and *Ymono i,j* is the stemwood yield of species *i* at year *j* growing in a monoculture. *Sp* is the species *i* proportion, calculated as the species density at year *j* (number of stems per hectare) in mixtures divided by the species density in a pure stand of the same species *i* simulated under the same climate scenario for the same year *j*. The *Ps* and *Fs* subscripts indicate pine and beech, respectively. Negative values of complementarity were interpreted as competition. Both equations are based on the selection and complementarity effects calculations proposed by Loreau & Hector (2001) and adapted by Forrester (2014). Alternative approaches to quantifying complementarity are also available (Fox 2005, Wu et al. 2015) but are not used in this study.

Two additional metrics of species performance were assessed including annual water use-efficiency (WUE) and nitrogen use-efficiency (NUE). WUE was determined as the ratio of net primary production (NPP, which was estimated as the sum of biomass increment, litterfall and mortality), to canopy transpiration (Sinclair *et al.* 1984). NUE was calculated as the ratio between NPP and the net uptake of nitrogen by each species (Lodhiyal et al. 1995). The above metrics were used to compare performance of: 1) pure and mixed stands under the historical climate scenario, and 2) mixtures with both historical and climate change scenarios.

3. RESULTS

3.1. Species interaction in historical climate simulations

In the case of the historical climate simulation, FORECAST Climate predicted a total yield in pine and beech mixtures of about 870 Mg ha^{-1} in the Mediterranean site and 550 Mg ha^{-1} in the continental site. In both sites, mixtures had higher yields than pure beech stands but lower than pure pine stands. An increasing temporal trend in stand-level complementarity as stands developed was found for the Mediterranean site. However, interaction effects between species in the continental site were weaker, starting with initial net competitive effects (negative complementarity) evolving over time towards facilitation (slightly positive complementarity, Fig. 3A). Annual stand productivity was greater in mature mixtures (over 100 years) at both sites (Fig. 4A). Yield complementarity and productivity patterns may be explained by improved nutrient status in mixtures compared to pure pine stands (Fig. 4B), lower water demand for transpiration (Fig. 4C), and higher NUE (Fig. 4D) for mixtures than for beech stands. In fact, nitrogen-leaching losses decreased 40% in the Mediterranean site and 75% in the continental site for mixtures relative to pure stands. Canopy precipitation interception of mixtures was close to that of pure pine stands while it was always lower than beech stands (Table 4). There were no differences in maximum rooting depth between the stands in either site. However, combined tree root occupancy of all soil layers was higher in mixtures than in pure stands.

Species-specific results show that complementarity was also greater in the Mediterranean site for both species (Fig. 3B; Table S7). Foliar nitrogen content per tree in pines was higher in mixtures than in pure stands (Fig. 5A). In mixed stands, crown length was 1.0 and 3.3 m greater than in mature

pure pine stands at the Mediterranean and continental sites, respectively. Although average pine transpiration per tree was higher in mixtures due to increased productivity (Fig. 5B) , no changes in WUE were predicted (Fig. 5D). In contrast, foliar nitrogen content per tree in beech was lower in mixed stands due to competition from pine (Fig. 6A). Therefore, simulated positive mixing effects on beech in the Mediterranean site were not light-related but associated with improved resource use efficiency (Fig. 6D).

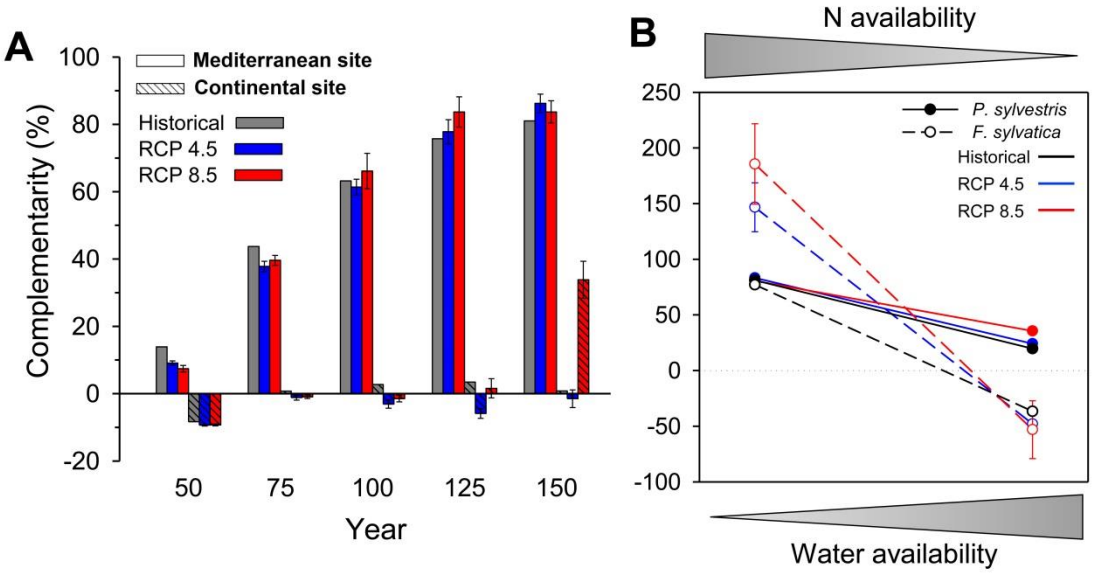

Figure 3. (A) Stand complementarity effects on stemwood yield calculated as in Eq. 3. (B) Species complementarity effects on stemwood yield at age 150 calculated following Eq. 2. The horizontal axis sums up resources gradients that occur between the two sites with different elevation (Mediterranean left side, continental right side).

Table 4. Percentage of precipitation intercepted by the canopy (mean ± SE) for stand age 50-150 years. Different superscripts mean statistically significant differences among stands types. Statistical comparisons were performed with univariate ANOVA.

	Historical	**RCP 4.5**	**RCP 8.5**
Mediterranean site			
Pine stands	15.77 ± 0.53^{a}	11.17 ± 2.45^{a}	12.45 ± 2.77^{a}
Beech stands	11.33 ± 0.43^{b}	7.96 ± 1.93^{b}	8.58 ± 2.08^{b}
Mixed stands	15.99 ±0.54^{a}	11.19 ± 2.35^{a}	11.98 ± 2.42^{a}
Continental site			
Pine stands	5.05 ± 0.27^{a}	4.20 ± 1.14^{a}	4.87 ± 1.33^{a}
Beech stands	3.78 ± 0.23^{b}	2.74 ± 0.90^{b}	3.07 ± 0.99^{b}
Mixed stands	4.64 ± 0.26^{a}	3.88 ± 1.11^{a}	4.63 ± 1.36^{a}

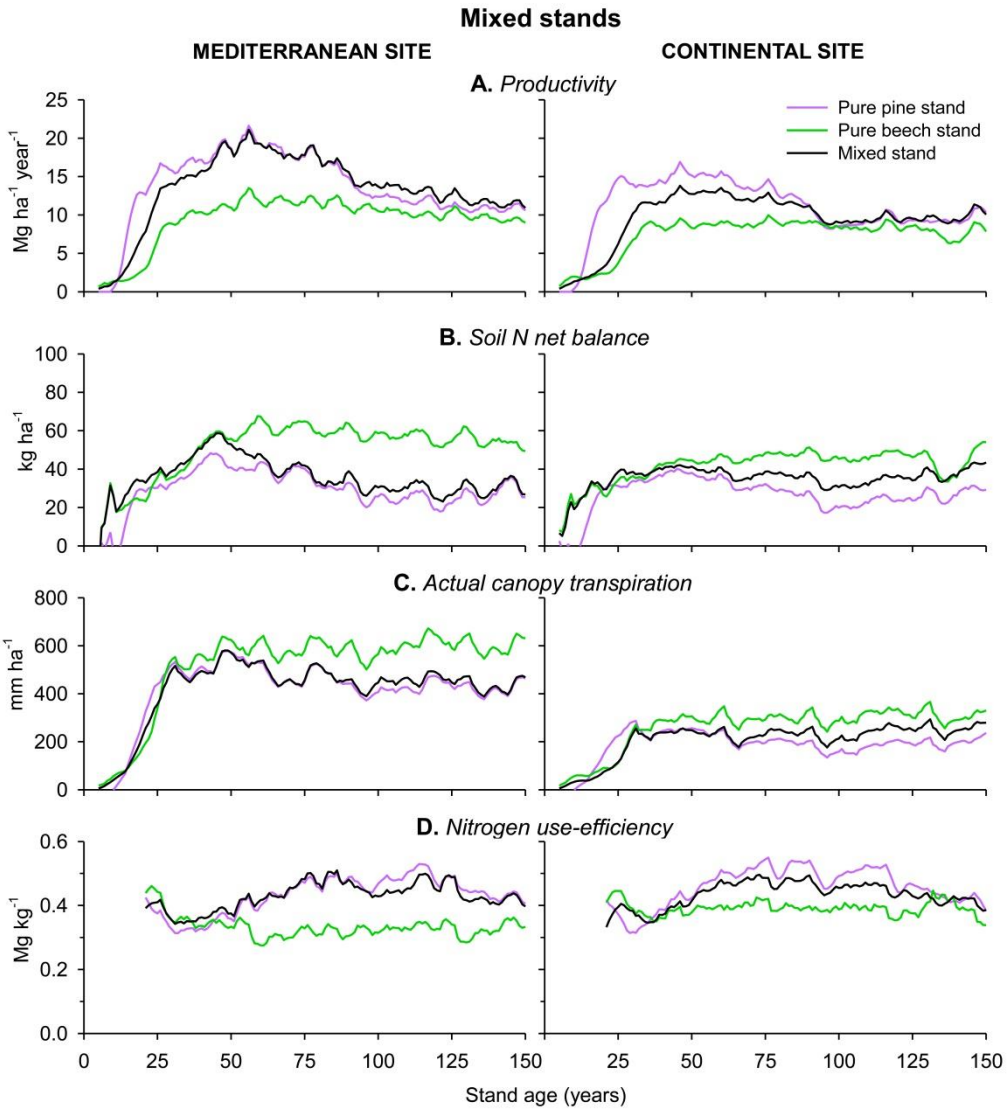

Figure 4. Stand level descriptors in pure *Pinus sylvestris* and *Fagus sylvatica* stands and pine/beech mixtures simulated under historical climate scenario. (A) Total stand growth per year (Mg ha^{-1} year^{-1}). (B) Soil nitrogen net balance (kg ha^{-1}) calculated as the difference between nitrogen released from litter and humus and leaching losses. (C) Actual stand canopy transpiration (mm ha^{-1}). (D) Ecosystem-level nitrogen use efficiency (Mg kg^{-1} N).

3.2. Impacts of climate change on ecological processes in mixed stands

Stand biomass accumulation under climate change (calculated as the average of moderate and severe climate change scenarios relative to the historical scenario) was significantly reduced in mixed stands in the Mediterranean site (-33%) and moderately increased in the continental site (+11%). This is consistent with the trends predicted for stand productivity, which decreased in the Mediterranean site and remained steady (or rising for the severe climate change scenario) in the continental site (Fig. 7A). Climate change had only minor impacts on stand complementarity, with the notable exception of the 150-year period at the continental site under severe climate change. At this site and time, complementarity increased substantially (Fig. 3A) following a period of drought-induced beech mortality. Predicted warmer temperatures led to accelerated decomposition of litter at both sites (Fig.

7D), but only at the continental site the net nitrogen balance increased (Fig. 7B). Stand-level canopy transpiration rates showed a minor increase in the climate change scenarios relative to the historical scenario at both sites (Fig. 7C). In contrast, warmer conditions and increased nitrogen mineralization at the continental site led to increased growth rates for both species. Moisture availability was not a limiting factor on growth in this site. Simulation results for the growth response index (GRI), TDI and drought-related mortality at the species-level are shown for mixed stands in Fig. S6.

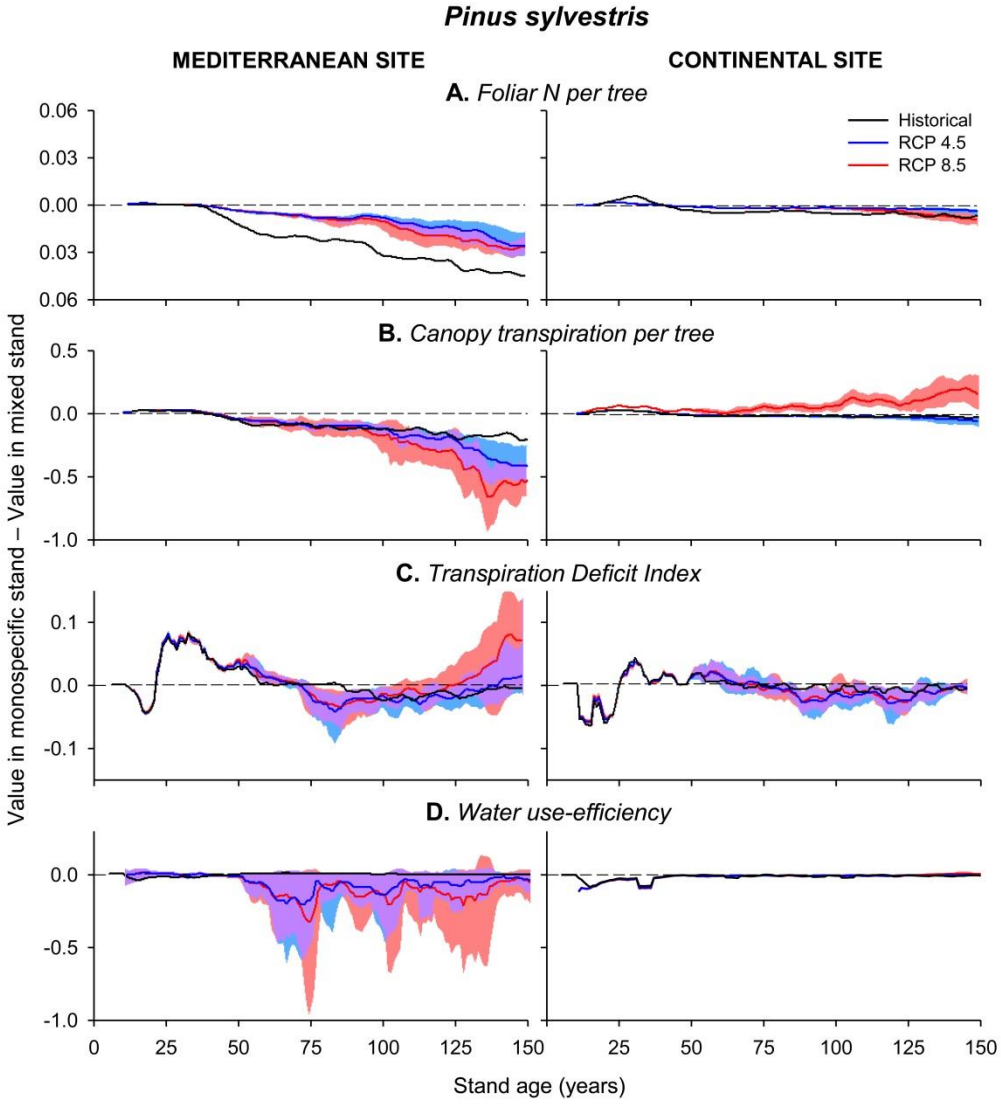

Figure 5. Differences between *Pinus sylvestris* output parameters in pure stands and mixed stands. Positive values indicate higher values in pure stands relative to mixtures. Thick lines represent average and color areas represent 95% and 5% percentiles; the purple area represents the overlap between the moderate (blue) and severe (red) climate change scenarios. (A) Amount of nitrogen accumulated in foliage biomass per tree (kg N $stem^{-1}$); (B) actual water transpired per tree (mm $stem^{-1}$); (C) transpiration deficit index (TDI) as a measure of water stress experienced by the species; (D) and water-use efficiency (WUE; Mg mm^{-1}).

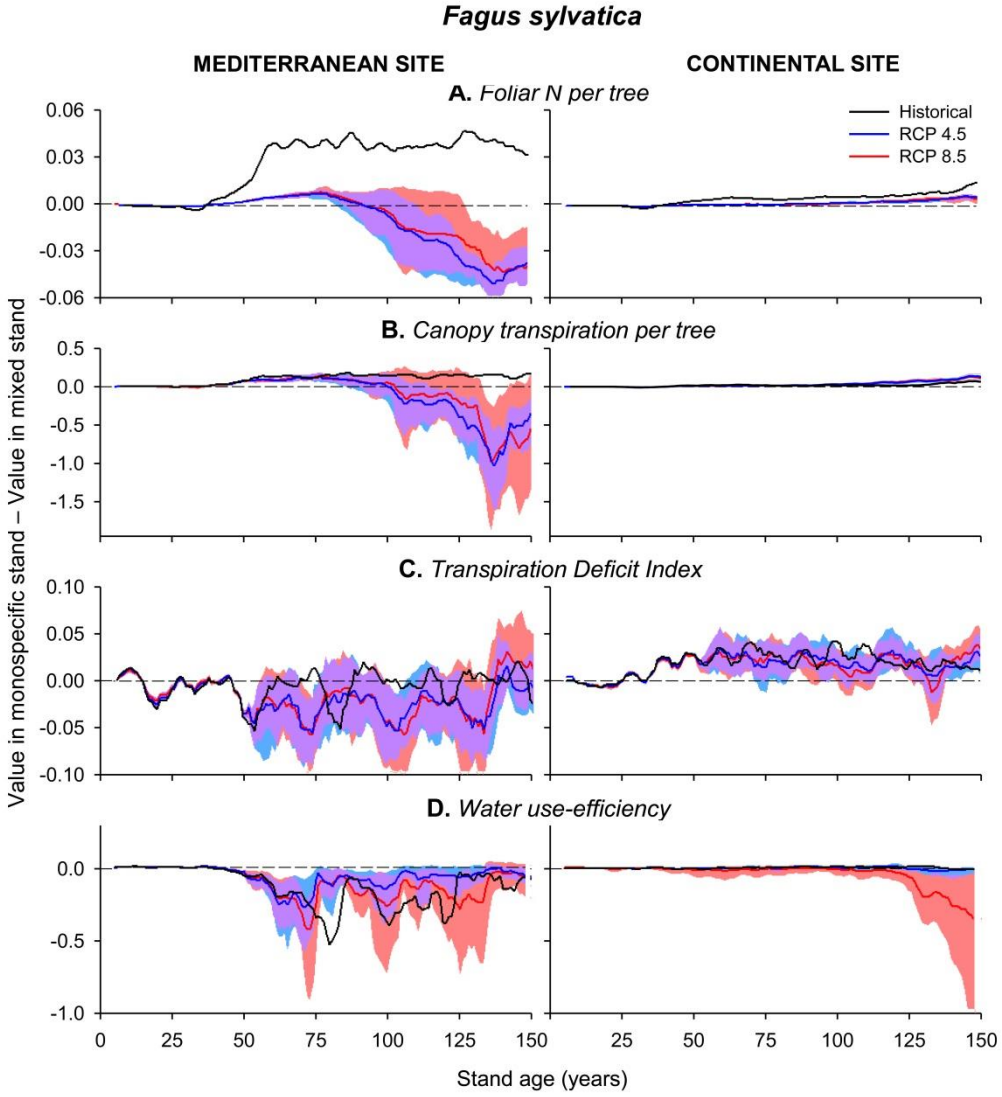

Figure 6. Differences between *Fagus sylvatica* parameters in pure stands and mixed stands. Positive values indicate higher values in pure stands relative to mixtures. Thick lines represent average and color areas represent 95% and 5% percentiles; the purple area represents the overlap between the moderate (blue) and severe (red) climate change scenarios. (A) Amount of nitrogen accumulated in foliage biomass per tree (kg N $stem^{-1}$); (B) actual water transpired per tree (mm $stem^{-1}$); (C) transpiration deficit index (TDI) as a measure of water stress experienced by the species; (D) and water-use efficiency (WUE; Mg mm^{-1}).

Complementarity for beech stemwood biomass increased as temperature and rainfall variability also increased in the Mediterranean site (Fig. 3B). Relative to pure stands, beech growing in mixtures under climate change showed increases in foliar nitrogen content and WUE, and concurrent reductions in water stress (Fig. 6). In contrast, complementarity for pine did not vary considerably in the climate change scenarios relative to the historical climate simulation. While the effects of mixing on foliage nitrogen content declined with climate change, WUE was greater for pines in mixtures relative to monocultures (Fig. 5). The relatively minor effects of mixing on light-, nutrient- and water-related processes in the continental site are consistent with limited complementarity levels also estimated for this site.

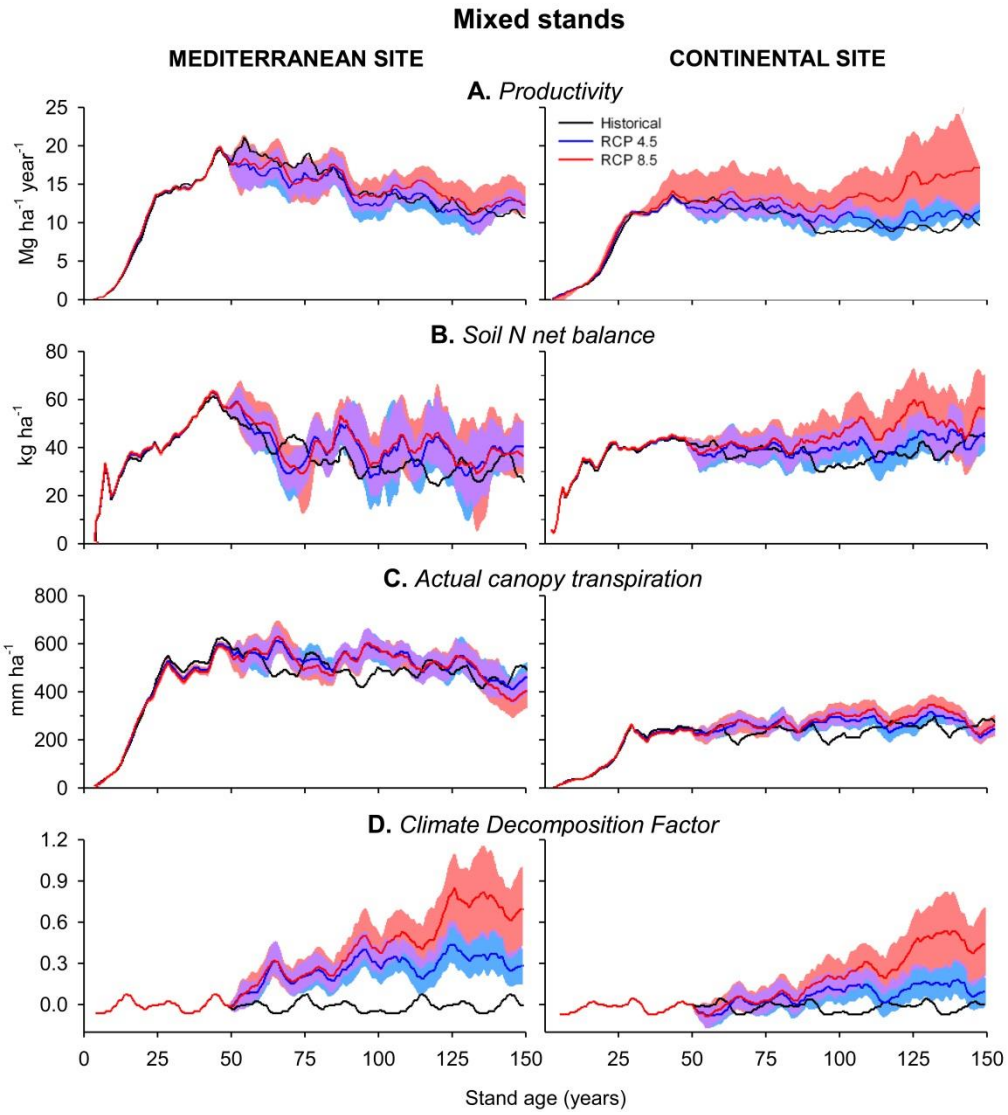

Figure 7. Stand level descriptors in *Pinus sylvestris* and *Fagus sylvatica* mixtures simulated in FORECAST Climate under different climate scenarios: historical, moderate (RCP 4.5) and severe climate change (RCP 8.5). Thick lines represent average and color areas represent 95% and 5% percentiles; the purple area represents the overlap between the moderate and severe climate change scenarios. (A) Total stand growth per year (Mg ha^{-1} $year^{-1}$). (B) Soil nitrogen net balance (kg N ha^{-1}) calculated as the difference between nitrogen released from litter and humus and leaching losses. (C) Total actual stand canopy transpiration (mm ha^{-1}) determined in the forest hydrology model ForWaDy. (D) Impact of climate on decomposition processes in the soil layers or Climate Decomposition Factor (CDF; dimensionless).

4. DISCUSSION

The prospect of climate change for the future survival and sustainability of beech has become of greater concern due to its high sensitivity to drought (Geßler et al. 2007). Pure pine stands also appear to be increasingly vulnerable to climate change, primarily because of the increased risk of insect outbreaks and fungal disease in such stands (Allen *et al.* 2010). Inter-specific differences in physiological and morphological traits provide advantage for pine-beech mixtures in terms of resource efficiency and overall resilience relative to pure stands (Pretzsch et al. 2015), particularly in the context of climate change. Although our modelling approach has some limitations (see below), it also has advantages that facilitate the analysis of potential impacts of climate change on key ecological processes, including nutrient and water availability, and efficiency of their use as well as the effects of different levels of species mixing, including proportions and total stand density (Río et al. 2014a, Blanco et al. 2015).

Differences between species growth rates were too large and mixing positive effects not big enough for stand biomass in mixtures to be greater than biomass in both pure stands. Nevertheless, complementarity effects (positive interaction) were predicted at stand- and species-levels for both sites. Facilitation, competitive reduction (considered jointly as complementarity) and competition in mixedwoods occur simultaneously. Changes in the importance of each factor have an influence on NPP. When species interactions improve the availability, uptake, or use efficiency of a resource that is becoming more limiting along the spatial or temporal gradient, complementarity also tends to increase along that gradient (Binkley et al. 2004, Forrester 2014). The stress gradient hypothesis (Bertness & Callaway 1994) has been recently considered as a special case that fits within the general 'complementarity – competition' framework (Forrester & Bauhus 2016). However, there are some differences between the 'complementarity – competition' framework and the stress gradient hypothesis. One difference is the nature of agronomic studies traditionally used to test the stress gradient hypothesis, whereas the ´complementarity – competition´ framework has been applied more often to forest ecosystems. Another difference is the consideration of facilitation and competitive reduction instead of just facilitation, or the difficulty to distinguish both processes occurring simultaneously in forests (Forrester & Bauhus 2016). In spite of these difficulties, several recent studies have successfully applied the stress gradient hypothesis to forest ecosystems in permanent environmental gradients or under episodic severe conditions (e.g. Pretzsch et al. 2012, Forrester 2014, Río et al. 2014a).

4.1. Understanding pine-beech interactions in the southwestern Pyrenees

Beech is known to have high drought sensitivity. Intensive summer droughts can significantly limit its growth and competitive ability (Geßler et al. 2007). Thus, greater complementarity effects on this species at the Mediterranean site compared with the continental site are consistent with the 'complementarity – competition' framework, as long as we consider water to exert a higher limitation than nutrients on beech growth. Supporting this assumption, Condés & Río (2015) found that water resources are of greater importance for beech than for pine in this region, increasing the effect of

competition for nutrients and light with higher precipitation in the same region. Such is the case of the continental site, where higher density might also promote competitive interactions.

Stress release of beech when mixed with different species has been reported in several studies (Pretzsch et al. 2012, Condés et al. 2013, Río et al. 2014a, b). Similarly, our results suggest that given the low self-tolerance of beech, complementarity may arise from processes that release intra-specific competition for water in mixtures. Transpiration is one of the key processes that influences water availability (Forrester 2015). Thus, the improvement in WUE in mixed stands suggests that beech may better tolerate drier conditions if grown in mixed stands relative to pure stands. Such result is in line with field observations at the Mediterranean site by Primicia et al. (2013), who reported beech radial growth reduction during the water stress season when mixed with pine.

In addition to transpiration, there are several simultaneous processes that could influence water availability and drought stress in mixtures (Forrester 2015). In FORECAST Climate, transpiration demand decreases as crown evaporation increases and energy is consumed in the process of crown evaporation (Seely et al. 2015). Thus, the simulated increase in the proportion of precipitation intercepted by the canopy of mixed stands compared to beech pure stands may partly explain the increase in WUE. The increase in interception rates in mixed stands is likely caused by the combination of: 1) higher LAI in coniferous forests than in broadleaves, 2) the contrasting canopy architecture of the two species that combined produce a more complete use of the canopy space than each species individually, and 3) the winter/early spring season when beech is defoliated but rainfall is important, which can therefore be intercepted by pine in mixed stands but not in pure beech woods (Fig. 2). In addition, belowground competition release could also improve water supply for beech in mixtures.

Water did not exert important limitation for pine growth, which seemed to be more dependent on light availability. Contrary to beech, pine growth and transpiration could have increased in response to processes that improve light and nutrient availability or uptake (Forrester 2015). Such mechanisms have been proposed to occur in the presence of beech for this species mixture in this region (Río et al. 2014b, Condés & Río 2015). The estimated spatial gradient in complementarity between our sites (which increased as nutrient supply improved) is also consistent with the 'complementarity – competition' framework, when light is considered the growth limiting resource for pine (Blanco et al. 2008, Forrester 2014, Forrester & Bauhus 2016).

Beech presence reduced aboveground intra-specific competition and improved nutrient supply for pine. Improvements in nutrient availability for pine in mixtures were more pronounced in the Mediterranean site and largely related to input from beech leaf litter. Compared to pine litter, beech litter has higher nutrient content, lower C/N ratio and less recalcitrant compounds, resulting in higher activity of soil microfauna and therefore higher litter decomposition rate, reduced soil acidity and a richer humus type (Kelty & Cameron 1995, Pretzsch et al. 2015). Non-symbiotic nitrogen fixation associated with beech litter also increased the available N content in mixed sites relative to pure pine sites. The resulting deeper canopies improved pine light interception in mixtures. In the continental site, nutrient availability is more limiting than in the Mediterranean site (Blanco et al. 2009, 2011) and, therefore, light-related complementarity was of lesser intensity. Competition for nutrients was

also probably encouraged by the high tree density predicted for the continental site, in accordance to data reported from similar sites in this region (Condés et al. 2013).

Inter-specific differences in resource requirements and uptake abilities often result in niche differentiation and resource-use complementarity (Richards et al. 2010). The hypothesis of more complete belowground exploitation (Río et al. 2014b, Pretzsch et al. 2015) was supported by our simulations through higher combined root occupancy in mixtures, which led to reduced nitrogen leaching losses and improved NUE at the stand level. A more efficient use of crown space due to contrasting light compensation points and light-use efficiencies (Preztsch et al. 2015), phenological differences (Schwendenmann et al. 2015) and contrasting patterns of stomata closure under drought conditions between species (Forrester 2015) have also been proposed as causes of complementarity in mixtures.

Recent studies based in the same region (Condés et al. 2013, Río et al. 2014b, Condés & Río 2015) similarly found water and light to be the primary limiting resource factors for beech and pine performance, respectively. However, our results illustrate the importance of also accounting for species interactions with respect to the dynamics of nutrient availability and uptake. This is particularly important for predicting future growth and ecosystem resiliency trends under different silviculture systems and climate scenarios.

4.2. Mixed stands projections under climate change

The temporal patterns of variation in complementarity observed in this analysis highlight the importance of using a long-term approach when evaluating tree interactions under different stress gradients. This variation is likely derived from temporal changes in climatic conditions or disturbances and modification of availability of light and soil resources by stand development (Forrester 2014). Our results point to the enhancement of interaction effects as stands develop over time. In the Mediterranean site, increasing stand complementarity was predicted for both species in mixtures. In the continental site, increasing complementarity and competition effects were predicted for pine and beech respectively. The projected trend of rising temperatures and increasing frequency of drought events (IPCC 2013) in southwestern Europe suggest that beech will increasingly benefit from associations in mixtures, particularly in areas with Mediterranean climates where it is expected to suffer growth reductions related to declining soil moisture and reduced nitrogen supply (Geßler et al. 2007). Messier et al. (2013) observed similar benefits for beech growing in mixtures in terms of increased forest resilience in the context of climate change.

Although pine is better adapted to dry conditions than beech and the main inter-specific interactions were nutrient- and light-related, the climate change simulations conducted here suggest that pine will also have better WUE when grown in a mixedwood condition. Regardless, water stress at the species-level was notably increased under climate change, because of the increased frequency of drought events, leading to higher drought-related mortality rates in the Mediterranean site. In any case, pine would also likely obtain greater additional benefits in mixtures from the mitigation of the susceptibility to secondary stress made by insects, fungi or windthrow damage caused by drought

(Allen et al. 2010, Pretzsch et al. 2015). All our results together point to the advantage of mixtures for both species at stand-level to face warmer environments with more frequent drought events.

4.3. Model advantages and limitations

All models have strengths and weaknesses that should be taken into consideration when evaluating model results. One of the strengths of the FORECAST Climate as tool for examining species interactions in mixed stands is that it does not use competition indices as proxies for species interactions. Rather, it includes explicit representations of above and belowground competition for available resources including nutrients, light and water, therefore allowing for an examination of shifts in inter-specific interactions across spatio-temporal environmental gradients (Río et al. 2014a). While such features enhance the capability of simulating species interactions (Blanco et al. 2015, Pretzsch et al. 2015), they also come with the cost of increased calibration data.

Some of the limitations of FORECAST Climate with respect to its application in mixed species stands include the following. There is neither representation of mycorrhizal relationships nor simulation of hydraulic redistribution in the model. Both of these can be important factors regulating ecosystem function in mixedwood forests (Neumann & Cardon 2012, Simard et al. 2012). In addition, drought-related mortality is empirically estimated based on pure stands, so the ability of the model to predict inter-specific interactions could be limited. Forrester (2015) showed that in mixtures not every tree of a given species present complementarity effects but only some of them grow faster than trees in pure stands and other trees grow at similar rates, and stand-level patterns will reflect the mean tree-level response. Thus, stand-level predictions could ignore potentially important individual tree responses. Additionally, the way in which density and species proportions are estimated could influence the calculation of complementarity. To address this issue, a species proportion definition that considers the different potential densities between species was chosen as it was referred to density in pure stands. This might provide more reliable estimation of mixing effects when there are differences in species potential densities (Sterba et al. 2014). A further limitation in our modelling approach could be attributed to the fact that the only nutrient considered was nitrogen. This assumption was based on previous research reporting that nitrogen is the main limiting nutrient at both sites (Blanco et al. 2008, 2009, 2011). However, recent findings suggest that phosphorous could also become limiting under some conditions at least in the Mediterranean site for pine growth (Primicia et al. 2014). Hence, further work is needed at conceptual, modelling, and empirical levels to include multi-nutrient limitations and interactions with other factors in the context of the ´complementarity – competition´ theoretical framework.

In spite of the aforementioned limitations, FORECAST Climate (and its predecessor FORECAST) has been successfully applied to a wide variety of situations (see Blanco et al. 2015, Lo et al. 2015, Seely et al. 2015, and references therein), including studies on complementarity and facilitation in tropical mixed plantations (see Table S2 and S3). This model has also been highlighted as one of the four more promising ecological models for its application in mixed forests, in a recent review encompassing 202 ecological models (Blanco et al. 2015). Such facts provide confidence in its suitability to simulate complex forest ecosystems.

5. CONCLUSIONS

In this study we provide insight towards a better understanding of inter-specific interactions in pine-beech mixedwoods growing close to their range limits. The results are also relevant across Europe as similar climate conditions may develop further north in more central distribution areas with climate change (Hampe & Petit 2005). The study provides support for increasing the establishment of pine-beech mixedwoods as an adaptation strategy to climate change in drought-prone sites. Our results suggest that the expected beneficial effect would be weaker at high elevation sites where water availability is not a key factor limiting growth. Complementarity of beech increased as water availability (major limitation for this species) declined. In the case of pine, interactions in mixtures were light-related, and complementarity was higher as nutrient supply improved and competition for belowground resources decreased. Thus, climate change was predicted to have a relatively smaller impact on pine grown in mixtures compared to beech. Our results are consistent with the 'complementarity – competition' framework as long as the limiting resources considered are water for beech and light for pine.

Our simulations highlight the key roles of water and nutrient availability and their interaction in the functioning of Scots pine - European beech mixed forests in the Pyrenees. On the one hand, the influence of water use and species interactions on tree growth has been already addressed with empirical data in Chapter 1. On the other hand, leaf litter constitutes a major proportion of nutrient cycling between trees and soils, so it can reveal limitations on internal fluxes of nutrients at ecosystem scale (McGroddy et al. 2004). Hence, the study of leaf litter mass and stoichiometry patterns in pine-beech mixtures along natural succession, together with their linkages with growth and water use of trees, may help to disentangle the combined effect of water and nutrient limitation. Such issues are tackled in Chapter 3.

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CHAPTER 3

Long-term leaf litter dynamics and N:P:K stoichiometry of Scots pine and European beech mixtures are connected with large-scale circulation patterns and secondary growth

Long-term leaf litter dynamics and N:P:K stoichiometry of Scots pine and European beech mixtures are connected with large-scale circulation patterns and secondary growth

ABSTRACT

Litterfall represents the main connection between vegetation and soils in terms of matter, nutrients and energy in forest ecosystems. Leaf litter dynamics (production, seasonality and nutrient composition) are key processes to better understanding functioning of mixed-species forests due to their large impact on nutrient return and thus nutrient limitation, which has direct and indirect effects on forest adaptation to global change. Leaf litter characteristics are greatly modified by species composition, site conditions and water availability, which are ultimately determined by large-scale circulation patterns (e.g. NAO, ENSO and PDO). Special attention is paid to N:P:K stoichiometry due to its linkage with important ecological processes. In order to achieve a more complete understanding of mixed forest ecosystem functioning, we aimed to establishe a conceptual framework linking leaf litter dynamics of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) mixtures with climate and other forest processes, such as tree-ring width (TRW) and intrinsic water-use efficiency (iWUE). We explored these relationships in two Scots pine – beech mixed stands with contrasting characteristics in the southwestern Pyrenees. Litterfall was collected monthly from August to November during a 16-year period. Temporal series of biomass and composition of nutrients were decomposed following the ensemble empirical mode decomposition (EEMD) method and relationships with local climate, large-scale climatic indices and TRW and iWUE of Scots pine were assessed. For both species leaf litter seasonality was better explained by ENSO, whereas NAO accounted for greater variation of nutrient composition. The influence of large-scale patterns was explained through their impact on water availability, as summer droughts induced premature pine needles' abscission and heavy rain in autumn hastened shedding of beech leaves. Apparently soil water conditions also modified nutrient availability, uptake, allocation and resorption, thus affecting leaf litter composition. Trends in N:P ratios pointed out an increasing P limitation of soil microbes, thus affecting nutrient release, in Pyrenean pine-beech mixtures. Relationships between leaf litter seasonality and Scots pine TRW and iWUE were found. Furthermore, pine TRW and iWUE responded to stoichiometry leaf litter fallen 3 years prior tree-ring formation. Overall, our results highlight the interactions between the impacts of water limitation and nutrient cycles on forest functioning.

Key words: ensemble empirical mode decomposition (EEMD), *Fagus sylvatica*, growth rate hypothesis, nutrient limitation, *Pinus sylvestris*, Pyrenees, stoichiometry

1. INTRODUCTION

Litterfall transfers organic matter, nutrients, and energy from the vegetation to the soils in forest ecosystems, and it is a dominant link in the biogeochemical cycling of matter (Vitousek 1982). Rates of decomposition and nutrient mineralization are driven by multiple factors, of which soils, climate, decomposer community, and litter quality are the most important (Berg & McClaugherty 2003, Parton et al. 2007). In two global meta-analyses, litter quality has been identified as the most important factor controlling decomposition rates and thus the resulting release of nutrients into the soil (Cornwell et al. 2008, Zhang et al. 2008). Litterfall can also characterise the properties of the underlying surface by changing the hydraulic conductivity and albedo (Liu et al. 1997), and impact the responses and feedbacks of terrestrial ecosystems to climate systems (Winkler et al. 2010). Thus, understanding the determinants of litterfall quantity and quality is a major issue in order to understand nutrient turnover in forest soils. It is a key parameter in measuring, modelling, and predicting forest ecosystem functioning.

The study of mechanisms and feedbacks that regulate nutrient distribution and transfer between different ecosystem compartments may provide insights into nutrient cycling and ecosystem nutrient limitation (Reed et al. 2012, Lang et al. 2016). Leaf litter constitutes (together with root turnover) a major proportion of nutrient cycling between plants and soils (Prescott 2002), and therefore it reflects constraints on internal fluxes at the ecosystem scale of carbon (C) and key element such as nitrogen (N), phosphorus (P) and potassium (K) (Vitousek 1982, McGroddy et al. 2004, Zechmeister-Boltenstern et al. 2015). N:P:K stoichiometry can be associated with important ecological processes and ecosystem traits, such as ecosystem composition and diversity (Güsewell et al. 2005), the ability of trees to adapt to environmental stresses (Sardans et al. 2013, 2017), or composition of decomposer communities and litter decomposition rates (Berg & McClaugherty 2003, Güsewell & Gessner 2009, Mooshammer et al. 2014).

One of the most widespread hypotheses in ecological stoichiometry is the growth rate hypothesis, which states that organisms must increase the relative allocation of P to P-rich ribosomal RNA to meet the elevated demands for protein synthesis required for rapid growth, which is possible under low N:P ratios in the environment (Sterner & Elser, 2002). This hypothesis has had consistent support in freshwater ecosystems (Sardans et al. 2012b and citations therein). However, in terrestrial plants those relationships remain inconclusive. Feedbacks between different organisms are also contemplated in ecological stoichiometry in the consumer-driven nutrient recycling theory. This theory predicts that the balance of the litter stoichiometry and soil decomposers microbes and their element use efficiency directly determine the ratios of nutrient recycling (Sterner & Elser 2002). Unlike plants, soil microbes are largely homeostatic in terms of C:N:P stoichiometry (Xu et al. 2013, Li et al. 2014). This means that variable resource stoichiometry has little or no effect on microbial biomass stoichiometry due to physiological regulation (Sterner & Elser 2002). Such regulation mainly includes the control of element use efficiencies and the production of extracellular C-, N- and P-acquiring enzymes (Mooshammer et al. 2014). The stoichiometric imbalance between litterfall and microbial communities results in the limitation of microbial activity by a particular nutrient, and thus the immobilization of that nutrient in microbial biomass. Therefore, leaf litter nutrients, particularly

N and P, strongly positively affect the decomposition rate due to the high demands of microbial decomposers for those nutrients to build and maintain biomass (Conrwell et al. 2008, Zechmeister-Boltenstern et al. 2015).

Nutrients and stoichiometry of leaf litter reaching the forest floor depend on leaf litter biomass, seasonality and nutrient concentrations. Year-to-year variations in climate and extreme weather events such as droughts or storms can importantly alter the dynamics and composition of litter production (Pausas et al. 1994, Yuan & Chen 2009a). Variations in leaf litter production have been explained by air temperature (Martínez-Alonso et al. 2007), rainfall (Lehtonen et al. 2008), soil temperature and moisture (Blanco et al. 2006), actual evapotranspiration (Berg & Meentemeyer 2001) or wind speed and early frost events (Portillo-Estrada et al. 2013), among others. Climate can also substantially impact on seasonal patterns of litterfall (Reich & Borchert 1984, Wright & Cornejo 1990, Portillo-Estrada et al. 2013, Zhang et al. 2014), thereby influencing soil microbial activity and nutrient cycles. As a result of modifications of leaf phenology and fall kinetics, there may be strong inter-annual differences in nutrients of senescent leaves (Killingbeck et al. 1990, Del Arco et al. 1991, Escudero et al. 1992, Niinemets & Tamm 2005).

Leaf litter nutrients are mainly determined by nutrient concentration in green leaves and the resorption processes during senescence (Killingbeck 1996, Kobe et al. 2005). There are substantial differences among species in nutrient composition of green leaves (Sardans et al. 2015) and leaf litter (Staelens et al. 2011, Yuan & Chen 2009a, Kang et al. 2010). Hence, forest species composition and canopy structure are pivotal drivers of decomposition and nutrient release. Mixed-species forests are increasingly receiving attention as they are considered more resistant to disturbances and extreme events (Jactel et al. 2017) and may provide ecosystem goods and services more effectively than pure stands (Gamfeldt et al. 2013, Duffy et al. 2017). Over recent decades in Europe, natural or managed growth of European beech (*Fagus sylvatica* L.) under Scots pine (*Pinus sylvestris* L.) canopy has progressively resulted in mixed stands. Although the scientific knowledge of the structure and functioning of this species mixture is quickly rising (*e.g.* Pretzsch et al. 2015, Metz et al. 2016, Barbeito et al. 2017, González de Andrés et al. 2017, 2018, Río et al. 2017), little is known about its litterfall dynamics and nutrient cycling. Rothe & Binkley (2001) reviewed multiple nutritional interactions in tree species mixtures regarding foliar nutrition, soil nutrient supply, and rates of nutrient input. Primicia et al. (2014) found an effect of inter-specific competition in resorption efficiency. Recently, Nickmans et al. (2017) have described a significant effect of neighbour species identity on leaf nutrient content. Furthermore, an effect of tree species richness on decomposition rates has been identified (Talkner et al. 2009, Joly et al. 2017). Consequently, nutrient cycling and limitation in mixed-species forests cannot be extrapolated from those of monospecific stands.

The assessment of climate-litterfall relationships has been traditionally focused on locally measured climatic components, but large-scale climatic circulations can partially capture the complexity and temporally variable associations between local climate and ecological processes and give an insight on the underlying mechanisms (Stenseth et al. 2002, 2003, Hallet et al. 2004). The dominant teleconnections (*i.e.* the simultaneous physical variations in climate over distant parts of the world) account for major variations in local weather and climate (Stenseth et al. 2002, Gámiz-Fortis

et al. 2011) since climate oscillations are related to changes in ocean temperatures and global atmospheric phenomena (Hurrell 1995). Indeed, several multiannual quasi-periodic oscillatory patterns have been identified, such as the North Atlantic Oscillation (NAO), the El Niño – Southern Oscillation (ENSO), and the Pacific Decadal Oscillation (PDO). The ability of large-scale indices to outperform proxies of local climatic conditions in explaining variation in ecological processes has been demonstrated in plant phenology (Post & Stenseth 1999, Guan 2014), or tree growth (Piovesan & Schirone 2000, Camarero 2011, Rozas et al. 2015, Lo et al. 2017, Madrigal-González et al. 2018). Nevertheless, to the best of our knowledge no research has analyzed the effect of global atmospheric-oceanic circulation patterns on leaf litter quantity and quality series.

Understanding productivity limitations imposed by nutrient availability, in which leaf litter dynamics play a key role, is increasingly important for forecasting forest ecosystem responses to global change (Sardans et al. 2017). Here, we aimed to analyze the leaf litter mass and composition from two mixed Scots pine – European beech forests of contrasting climatic and fertility characteristics of the western Spanish Pyrenees over a 16-year period. Our specific objectives were (1) to estimate the trends in possible ecosystem nutrient limitation using leaf litter nutrient concentration and stoichiometry series as they may constraint further decomposition and nutrient release; (2) to assess the relationships between leaf litter dynamics and trees' performance regarding water-use efficiency and secondary growth; and (3) to evaluate the influence of local climate and large-scale circulation patterns on leaf litter production and nutrient composition of both species in order to improve our knowledge of environmental controls of biogeochemical cycling at the ecosystem level. We hypothesize that (1) leaf litter stoichiometry influences secondary growth of Scots pine, and (2) prevailing large-scale climatic indices (*i.e.* NAO, ENSO, and PDO) will correlate with variations in amounts and compositions of leaf litter mediated by water availability, a key factor for southern rear-edge populations of Scots pine and beech.

2. MATERIAL AND METHODS

2.1. Study area and climatic data

The study area is located in the southwestern Pyrenees, northern Spain (province of Navarre). Two contrasting sites have been considered: a sub-xeric site located at low elevation with a cool and wet Mediterranean climate (MED site), and a mesic site situated at high elevation and characterized by cold-wet continental climate (CONT site). Both forests are even-aged Scots pine stands resulting from successful natural regeneration after clear-cuttings carried out in the early and mid-1960s. Over recent decades, European beech growth under pine canopy has progressively resulted in mixed stands, particularly at the Mediterranean site. Further information on site characteristics and stand structure is provided in Table 1. Data describing soil characteristics were obtained by digging soil pits from each site and are shown in Table 2.

In order to evaluate the impact of climatic conditions on leaf litter dynamics, radial growth, and water-use series, daily historical climate data (maximum and minimum temperature and precipitation) for a 40-year period (1975-2015) were obtained from the nearest weather stations to each site. Due to the large elevation difference between the continental site and the closest weather

station (over 600 m), the mountain microclimate simulation model MT-CLIM (Running et al. 1987) was applied to correct climate data (Lo et al. 2011). Maximum and minimum temperature lapse rates and precipitation isohyets needed for extrapolation were calculated from regional climate data. Missing data were calculated by interpolating values from nearby weather stations.

Table 1. Sites and stands characteristics (mean ± standard error) measured in 2014. Stands descriptors were taken from Puertas (2001) and Iriarte and Puertas (2003).

Site	Mediterranean site	Continental site
Latitude	42º42'31'' N	42º48'50'' N
Longitude	1º8'40'' W	52'30'' W
Altitude (m a.s.l.)	625	1335
Climate type (Papadakis, 1970)	Cold wet Mediterranean	Cold wet continental
Mean annual temperature (º C) [a]	11.9 ± 0.1	9.4 ± 0.1
Total annual precipitation (mm) [a]	922 ± 25	1346 ± 61
Soil	Haplic Alisol	Dystric Cambisol
Slope (%)	7	40
Density (stems ha^{-1}) [b]	2400 ± 301	2019 ± 212
Total basal area (m^2 ha^{-1})	57.5 ± 2.25	56.0 ± 6.3
Tree species richness	18	10
Density proportion of *P. sylvestris* (%)	69.34 ± 0.02	85.22 ± 0.06
Density proportion of *F. sylvatica* (%)	11.73 ± 0.04	13.71 ± 0.05
Site Index at stand age 80 years (m) [c]	29	23
Age (years) [c]	47	51
Dominant height (m) [c, d]	20.4 ± 0.3	17.3 ± 0.9
Mean dbh *P. sylvestris* (cm) [e]	17.2 ± 1.1	17.9 ± 0.8
Mean dbh *F. sylvestris* (cm) [e]	8.5 ± 0.5	5.0 ± 1.1

[a] Referred to the period 1980-2015.
[b] Trees with a diameter at breast height (1.30 m, dbh) > 7.5 cm.
[c] Referred to *P. sylvestris*.
[d] Measured averaging (n = 100) the height of the thickest dominant trees per hectare.
[e] Measured by double cross measurement.

Monthly local climate data were transformed into a more biologically meaningful variable that informs about soil water condition: the standardized precipitation evaporation index (SPEI). The SPEI.*X* is a multi-scalar index, where *X* refers to the time scale in months at which it is calculated. This index includes both precipitation and temperature influence in droughts by means of the evapotranspiration processes (Vicente-Serrano et al. 2010a). It has shown an improved capability to identify drought impacts when compared with other commonly used drought indices (e.g. Vicente-Serrano et al. 2012). The SPEI is based on a monthly climatic water balance (precipitation minus potential evapotranspiration, PET), which is adjusted using a three-parameter log–logistic distribution. PET was estimated following Thornthwaite & Mather (1957) and the *SPEI* package (Beguería & Vicente-Serrano 2017) from R software was used to calculate SPEI at time scales from 1 to 6 months.

In order to identify the responses of local climate and leaf litter dynamics to large-scale circulation patterns, we considered three monthly atmospheric-oceanic oscillatory patterns. The NAO Gibraltar-Stykkihólmur (NAO) refers to a north-south alteration in atmospheric mass between the subtropical Atlantic and the Arctic and its fluctuations are of greatest amplitude during the cold season months (Osborn 2011). ENSO describes the atmosphere-ocean interactions throughout the tropical Pacific and represents the strongest inter-annual variation of Earth's climate affecting a wide range of geographic areas (Stenseth et al. 2003). In this study we focused on NIÑO12 (0ºN-10ºS, 90ºW-80ºW; Cimate Prediction Center, NOAA, http://www.cpc.noaa.gov/data/indices). PDO is an inter-decadal variation of the atmosphere-ocean interphase in the North Pacific (http://jisao.washington.edu/pdo).

Table 2. Topsoil physical and chemical properties (mean ± SE) in the study sites sampled along the litterfall collection period 2000-2015 (11 sampling dates).

	Mediterranean site	**Continental site**
Texture [a]	Silt loam	Loam
Density (g cm^{-3})	0.96	0.76
pH 1:2.5 H_2O	5.05 ± 0.06	5.20 ± 0.05
CEC ($cmol^+ kg^{-1}$)	11.21 ± 0.39	20.19 ± 1.38
O.M. (%)	9.22 ± 0.41	9.57 ± 0.62
C (mg g^{-1})	53.12 ± 2.75	52.62 ± 2.36
N (mg g^{-1})	2.62 ± 0.12	2.39 ± 0.08
P (mg g^{-1})	0.018 ± 0.001	0.025 ± 0.002
K (mg g^{-1})	0.114 ± 0.004	0.146 ± 0.007
C/N	20.68 ± 0.51	22.43 ± 1.13
N/P	196.9 ± 13.9	139.3 ± 22.4

[a] Based on USDA classification.

2.2. Litterfall sampling

Three unmanaged plots (30 m x 40 m) were set up at each study site. The collection of aboveground litterfall involved the installation of 9 circular litter traps (0.6 m diameter and 1 m height) randomly distributed in each plot. A conical plastic mesh was attached to the structure, with 1.5 mm mesh size and 0.5 m depth. The litterfall samples deposited in each trap were collected during the first week of each month from September to December in the Mediterranean site and from September to November in the continental site (heavy snowfalls commonly prevented litter collection at this site from the first week of December onwards). This period was selected as it comprises the main aboveground litterfall peak of pine needles and beech leaves at the study sites (Blanco et al. 2006). Every trap was emptied in the beginning of August. Litterfall collection was conducted over a 16-year period (2000 – 2015). Samples were air dried for 24 h, and dried at 70 °C in a drying oven to constant weight. Samples were weighed on a precision scale and separated into five fractions: Scots pine needles, European beech leaves, leaves of other broadleaf species, pine branches, and miscellaneous (bark, cones, beechnuts, buds, inflorescences, etc.). Then, their dry weights were determined and they were scaled up to represent a unit area (kg ha^{-1}) for the forest as a whole.

Leaf litter (pine needles and beech leaves) samples were pooled by plot and year and grounded through a 1-mm sieve (MF-10, IKA). Total nitrogen concentration ([N]) in leaf litter was determined

by the dry combustion Dumas method (Matejovic 1993) using a TRUSPEC CN628 elemental analyzer (LECO Corporation, MI, USA). Concentration of other major elements phosphorus ([P]) and potassium ([K]) were measured using inductively coupled plasma emission spectrometry (ICP–ICAP 6500 DUO Thermo, England), after acid digestion (HNO_3–H_2O_2 4:1) in a microwave.

2.3. Scots pine radial growth and water-use efficiency

At each location, we randomly chose eight dominant and co-dominant pine trees per plot (n = 50). Selected trees were sampled at breast height perpendicular to the maximum slope using a Pressler increment borer. Sampling was conducted in the beginning of 2014. Two complete radii were extracted from each tree. Cores were air dried, glued onto wooden mounts, and sanded until tree rings were clearly visible (Fritts 2001). All samples were visually cross-dated using the identification of signature years. Tree-ring width (TRW) was measured to a precision of 0.01 mm using a LINTAB measuring device (Frank Rinn, Heidelberg, Germany). Cross-dating was further validated using the COFECHA software, which calculates moving correlations among individual tree series (Holmes 1983). For each tree, measurements from the two cores were averaged.

We used $^{13}C/^{12}C$ isotope ratios in wood from cross-dated cores as proxies of the intrinsic water-use efficiency (iWUE). Isotopic discrimination in C3 plants is a result of the preferential use of $^{12}CO_2$ over $^{13}CO_2$ during photosynthesis. The two stable C isotopes are incorporated in varying amounts depending on the ratio between the intercellular (C_i) and the atmospheric CO_2 concentrations (C_a), which is, in turn, determined by stomatal conductance (Farquhar et al. 1982). We randomly chose five trees at each study site (n = 10) among trees previously selected for growth analysis. The procedure followed for C isotopic analysis and iWUE calculation has been described in a previous publication (see González de Andrés et al. 2018).

Mean chronologies of TRW and iWUE of Scots pine were constructed by averaging individual tree chronologies at both plot and site scales for the period 2000-2013.

2.4. Time series decomposition

In order to avoid spurious relationships between climatic and ecological variables that may arise from strong temporal dependence (Stenseth et al. 2003), we decomposed climatic and leaf litter production and nutrient composition series into oscillatory component (OC) and trend by means of ensemble empirical mode decomposition (EEMD). EEMD is an improvement of empirical mode decomposition (EMD), an empirical but highly efficient and adaptive method for processing non-linear and non-stationary signals (Huang et al. 1998, Huang & Wu 2008). This methodology has been demonstrated to have great potential for chronology development as EEMD decomposed series better correlate with instrumental data than chronologies obtained following classic detrending methods (Guan et al. 2018).

EMD aims to decompose a time series into a small number of oscillatory components (intrinsic mode functions, IMFs) and a residual (trend) component (Huang et al. 1998; Huang and Wu 2008). The IMFs are sequentially extracted from high to low frequencies using a spline-based iterative sifting process. Once an IMF is extracted, EMD subtracts it from the time series and sifts through the

remaining part of the signal to extract the next IMF of lower frequency until it cannot find one. The remaining signal (trend) is either constant, monotonic, or with only one extremum (Huang et al. 1998; Huang & Wu 2008). Developed to alleviate the signal intermittence problem in EMD, EEMD is a Monte Carlo process in which zero-mean Gaussian white noise is added to each EMD process to achieve better signal separation (Wu & Huang 2009). Detailed description of EMD and EEMD can be found in Huang et al. (1998), Huang & Wu (2008) and Wu & Huang (2009).

EEMD has been successfully applied to dendrochronological (*e.g.* Guan et al. 2012, Zhang & Chen 2017, Lo et al. 2017, Guan et al. 2018) and phenological data (Guan 2014). EMD-EEMD decomposes time series based on local behaviors and in a sequential manner, thus it does not assume either linearity or stationarity in data. The trend is derived intrinsically and adaptively, so it does not require an *a priori* structure (Wu et al. 2007). These properties make EEMD an ideal tool for separating OCs from the trend (Guan 2014).

The decomposition was conducted using *Rlibeemd* package (Helske & Luukko 2016) from R software. Each EEMD run comprised 5000 EMD runs. The standard deviation of the introduced Gaussian white noise was 0.1 of that of the average climatic and leaf litter production and composition series. For EEMD decomposition, each series was decomposed into an oscillatory component (the sum of the EEMD IMFs) and a trend. EEMDs of leaf litter variables were performed using averaged series at species and site level.

2.5. Statistical analyses

Between-sites and between-species differences in production of different litterfall fractions and nutrient concentrations and ratios, as well as identification of litterfall production peaks during fall season were assessed with one-factor ANOVA. Linear mixed effects models (LMMs) were used to evaluate the effect of site or month (fixed factors) with plot nested in year as a random effect and a correlation structure to account for the repeated measures on the same plot. Differences between months were assessed with Tukey´s post hoc comparisons.

Redundancy analyses (RDA) were performed to assess the influence of local climate and large-scale circulation indices on leaf litter dynamics from 2000 to 2015 based on experimental plots as cases and considering both sites together. Oscillatory components (OCs) of monthly leaf litter production and composition (N:P:K concentrations and stoichiometric relationships) were considered as response matrices. Predictive matrix included SPEI, large-scale circulation indices (NAO, ENSO and PDO) and year to control for repeated measures on the same plot. Time scale (number of months considered for index calculation) and time-lag (number of years prior leaf abscission) were selected based on previous maximum cross-correlations. We considered meaningful relationships with large-scale circulation indices as long as they were consistent with local climate variables. Associations between pine needle litter composition and climate were assessed up to 4-year lagged climate variables. Variation partitioning was used to estimate the variance explained by local climate, large-scale patterns and time, as well as the covariance between them (Brocard et al. 1992, Peres-Neto et al. 2006). We then performed spatiotemporal correlations of local climate and leaf litter variables with two detrended monthly gridded fields: HadISST1 dataset (a reconstructed 1º x 1º sea surface

temperature (SST) field; Rayner et al. 2003), and NCEP/NCAR dataset (a reanalysis of 2.5º x 2.5º sea level pressure (SLP) field; Kalnay et al. 1996).

The relationships between leaf litter dynamics, water use and Scots pine tree growth were evaluated by means of principal component analysis (PCA) based on experimental plots as cases and considering the effect of the factor 'Year'. All variables were standardized in order to avoid biases due to magnitude differences. Firstly, the connection of monthly pine needle litter production with TRW and iWUE of the same year was assessed. Secondly, the relationship among leaf litter quality and pine TRW and iWUE was analized considering the joint contribution of both species to leaf litter. So for each species, concentration of nutrients was multiplied by the annual leaf litter biomass and then the nutrient content of both species was added. Time-lag between leaf litter fall and TRW and iWUE (i.e. delay in years from leaf abscission to maximum effect on tree-ring formation) was assessed using LMMs, considering up to 5-year lagged leaf litter shedding. Models included nutrient content, stoichiometric relationships and site as fixed factors, as well as a random intersection associated with plot nested in year (random factor) and a first-order autocorrelation structure.

LMMs and post hoc comparisons were carried out using *nlme* (Pinheiro et al. 2017) and *multcomp* (Hothorn et al. 2008) packages from R software, respectively. Likewise, RDA and PCA analyses were conducted with *vegan* package (Oksanen et al. 2017). Cross-correlations and spatiotemporal correlations were conducted via the Royal Netherlands Meteorological Institute Climate Explorer website (http://climexp.knmi.nl/) (Trouet & Van Oldenborgh 2013).

3. RESULTS

3.1. Litterfall production and composition varied with species, sites, and climatic conditions

Leaf organs were the most important aboveground litterfall fraction at both sites: Scots pine needles, beech leaves and leaves from other broadleaf species at the Mediterranean site and pine needles at the continental site, accounted for more than 70 % of total littefall at both sites (Table 3). Although no significant differences were found in autumn pine needle production between sites (ANOVA, $F = 2.846$, $p = 0.167$), beech leaves ($F = 23.318$, $p = 0.008$), leaves of other broadleaf species ($F = 8.414$, $p = 0.044$), pine branches ($F = 31.755$, $p = 0.005$) and miscellaneous ($F = 8.364$, $p = 0.044$) fractions were higher at the Mediterranean site. Leaf litter dynamics were observed to shift from pine dominated to pine and beech co-dominated canopy at the Mediterranean site, whereas the continental canopy remained dominated by the pine during the whole study period (Fig. 1A).

Table 3. Litterfall production (mean ± standard error; kg ha^{-1}) of late summer and autumn at both study sites separated by months, fractions and localities. Different letters correspond to significant differences among months within litterfall fraction and site ($p < 0.05$, Tukey test).

	Site	Total	Aug	Sep	Oct	Nov	*F*	*p*-value
Scots pine needles	MED	1285.6 ± 73.6	495.5 ± 46.2 a	453.7 ± 57.6 a	240.0 ± 26.7 b	96.4 ± 12.4 c	91.41	<0.0001
	CONT	1627.9 ± 98.5	341.5 ± 77.1 a	570.0 ± 59.3 b	716.4 ± 99.3 b		16.79	<0.0001
Beech leaves	MED	552.8 ± 48.3	11.9 ± 2.1 a	20.1 ± 4.2 a	124.6 ± 32.8 b	396.3 ± 51.5 c	103.02	<0.0001
	CONT	7.4 ± 1.3	0.7 ± 0.6 a	0.5 ± 0.2 a	6.2 ± 1.1 b		36.38	<0.0001
Other broadleaves	MED	156.6 ± 48.7	16.4 ± 5.0 a	15.8 ± 5.6 a	67.4 ± 30.5 a	65.4 ± 11.8 b	7.01	0.0002
	CONT	14.3 ± 7.7	3.6 ± 1.6 ab	2.7 ± 1.3 a	7.8 ± 5.2 b		3.74	0.0274
Scots pine branches	MED	423.2 ± 74.4	184.4 ± 49.9 a	106.8 ± 37.6 ab	83.2 ± 28.0 b	48.7 ± 19.4 b	5.56	0.0012
	CONT	116.1 ± 31.3	56.1 ± 27.1 a	26.2 ± 10.1 a	33.9 ± 7.3 a		2.07	0.1321
Miscellaneous	MED	401.9 ± 51.1	172.8 ± 28.4 a	87.6 ± 17.6 bc	101.6 ± 22.9 b	50.7 ± 18.2 c	13.40	<0.0001
	CONT	254.4 ± 38.5	127.0 ± 32.3 a	58.6 ± 7.5 bc	68.8 ± 10.2 c		11.00	0.0001

Table 4. Nutrient concentration and ratio of nutrients (mean ± standard error) of leaf fractions of litterfall of Scots pine (*Pinus sylvestris*) and European beech (*Fagus sylvatica*) at the two study sites: Mediterranean site (MED) and continental site (CONT). Significant differences between sites ($p < 0.05$, ANOVA) is shown with asterisks.

	Pinus sylvestris		*Fagus sylvatica*	
	MED site	CONT site	MED site	CONT site
[N] (mg g^{-1})	7.14 ± 0.34	6.24 ± 0.25*	14.04 ± 0.58	9.45 ± 0.47*
[P] (mg g^{-1})	0.23 ± 0.01	0.39 ± 0.01*	0.36 ± 0.02	0.45 ± 0.03
[K] (mg g^{-1})	2.33 ± 0.12	2.34 ± 0.11	5.22 ± 0.34	3.52 ± 0.33*
N:P	31.88 ± 1.19	16.28 ± 0.53*	40.02 ± 1.57	22.81 ± 1.11*
N:K	3.10 ± 0.11	2.79 ± 0.12	2.85 ± 0.13	3.41 ± 0.28
P:K	0.099 ± 0.003	0.173 ± 0.006*	0.077 ± 0.006	0.158 ± 0.014*

Leaf litter production varied significantly during autumn season (Table 3). Pine needles fall displayed a peak between August-September at the Mediterranean site however the peak was relatively delayed at the continental site to September-October. Meanwhile, massive beech leaf abscission was later than pine needles' peaks: November at the Mediterranean site and October at the continental site. A decreasing trend of needle litter production during early autumn months and a striking increase of beech leaves in November were observed at the Mediterranean site (Fig. 1B). The magnitude of beech leaf litter production was lesser at the continental site (Fig. 1C).

All nutrient concentrations were significantly higher in beech leaves than in pine needles ([N]: $F = 41.99$, $p = 0.001$; [P]: $F = 12.93$, $p = 0.015$; [K]: $F = 26.65$, $p = 0.004$). Between-site differences in nutrient concentration of leaf litter varied depending on nutrient and species (Table 4). Significant differences ($p < 0.05$) between sites were found fo [N] (MED site > CONT site) and [P] (Med site < CONT site) in pine needle litter, and for [N] (MED site > CONT site) amd [K] (MED site > CONT site) in beech leaf litter (Table 4). [N] and [P] displayed contrasting temporal trends, increasing in the former element and decreasing in the latter one (Fig. 2A and 2C). N:P ratio of leaf litter was greater at the Mediterranean site, while the opposite pattern was found for P:K ratio (Table 4). Overall, N:P ratios showed a rising trend (Fig. 2D), while P:K ratios displayed a general decrease (Fig. 2F). No clear trends were found in N:K ratios (Fig. 2E).

SPEI during summer was negatively related with pine needle litter produced in August (Fig. 3A). That is, the higher the soil moisture during summer the later the needles fall. Beech leaf fallen in September and October was positively related with $SPEI.1_{September}$, and the association was negative with November leaf litter (Fig. 3B). [N] and [P] of pine needle litter showed positive relationships with late spring and early summer water availability of 3 years prior needle abscission (Fig. 3C). [P] of beech leaf litter positively responded to water availability during summer, while the response was negative for [K] (Fig.3D). Stoichiometric relationships of both species at the two sites responded homogeneously to water availability. Dry conditions in late spring and summer increased N:P and reduced N:K and P:K ratios.

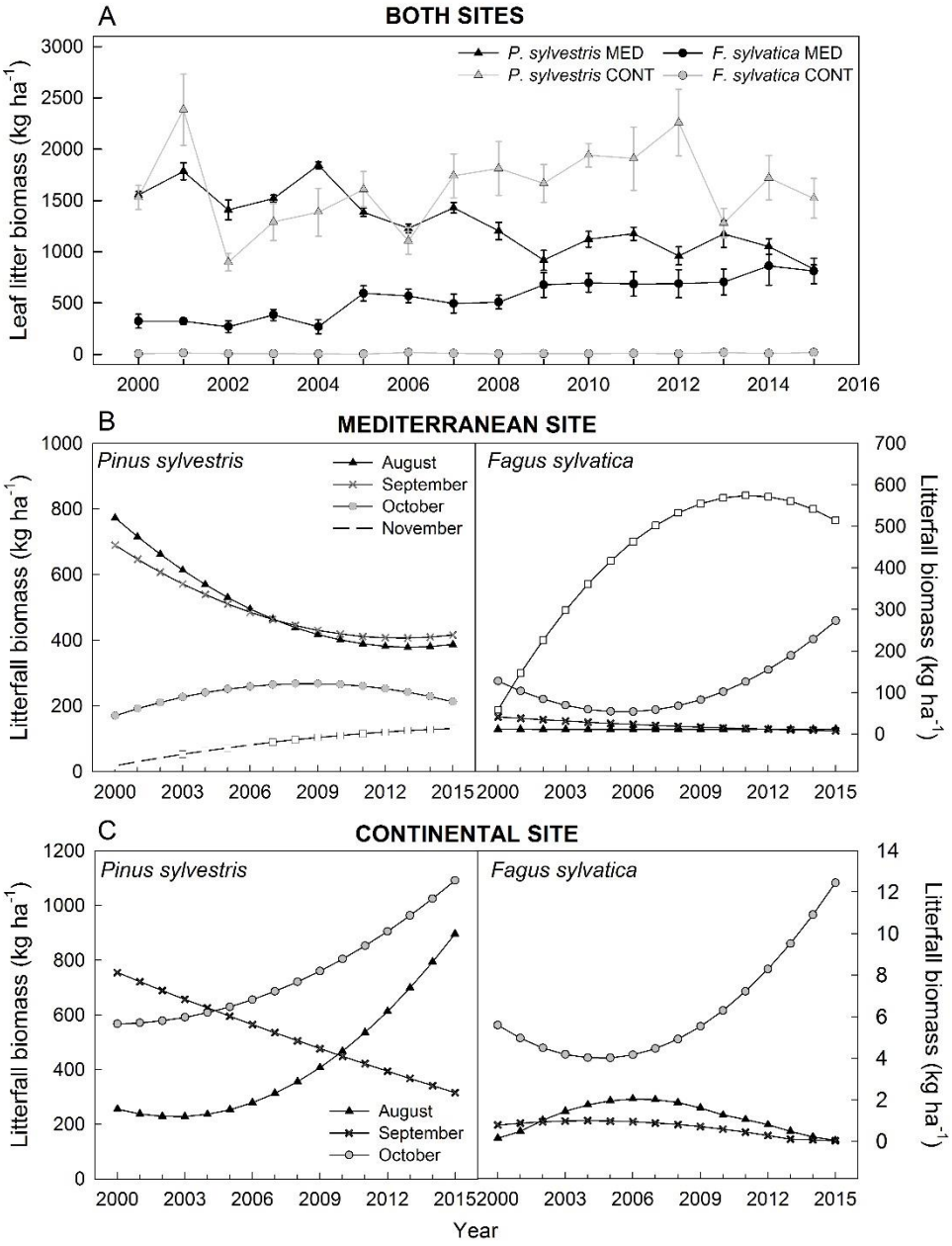

Figure 1. Evolution of whole-fall leaf litter biomass (A) and trends of monthly leaf litter production at the Mediterranean site (B) and continental site (C). Trends were extracted by means of ensemble empirical mode decomposition (EEMD) (see section *2.4.*). Different symbol represent different months.

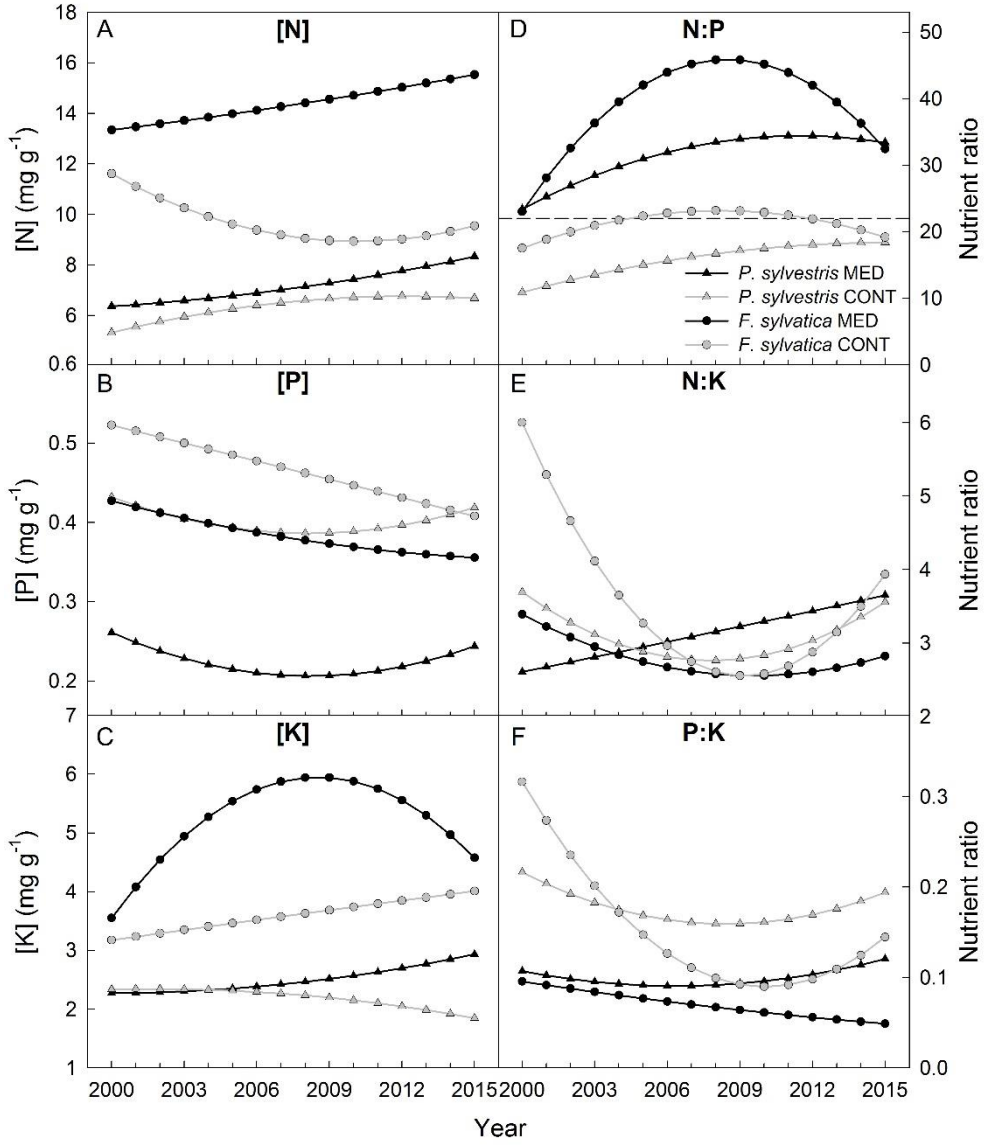

Figure 2. Trends of different ratios of nutrient concentration of Scots pine needles (*Pinus sylvestris*, triangles) and European beech leaves (*Fagus sylvatica*, circles) in the litterfall collected at the two study sites: Mediterranean site (MED, black) and continental site (CONT, grey). Trends were extracted by means of ensemble empirical mode decomposition (EEMD) (see section *2.4.*). Horizontal dash line in D graph represents the threshold value of N:P above which litterfall decomposition has been proposed to be P-limited (Güsewell & Freeman 2005).

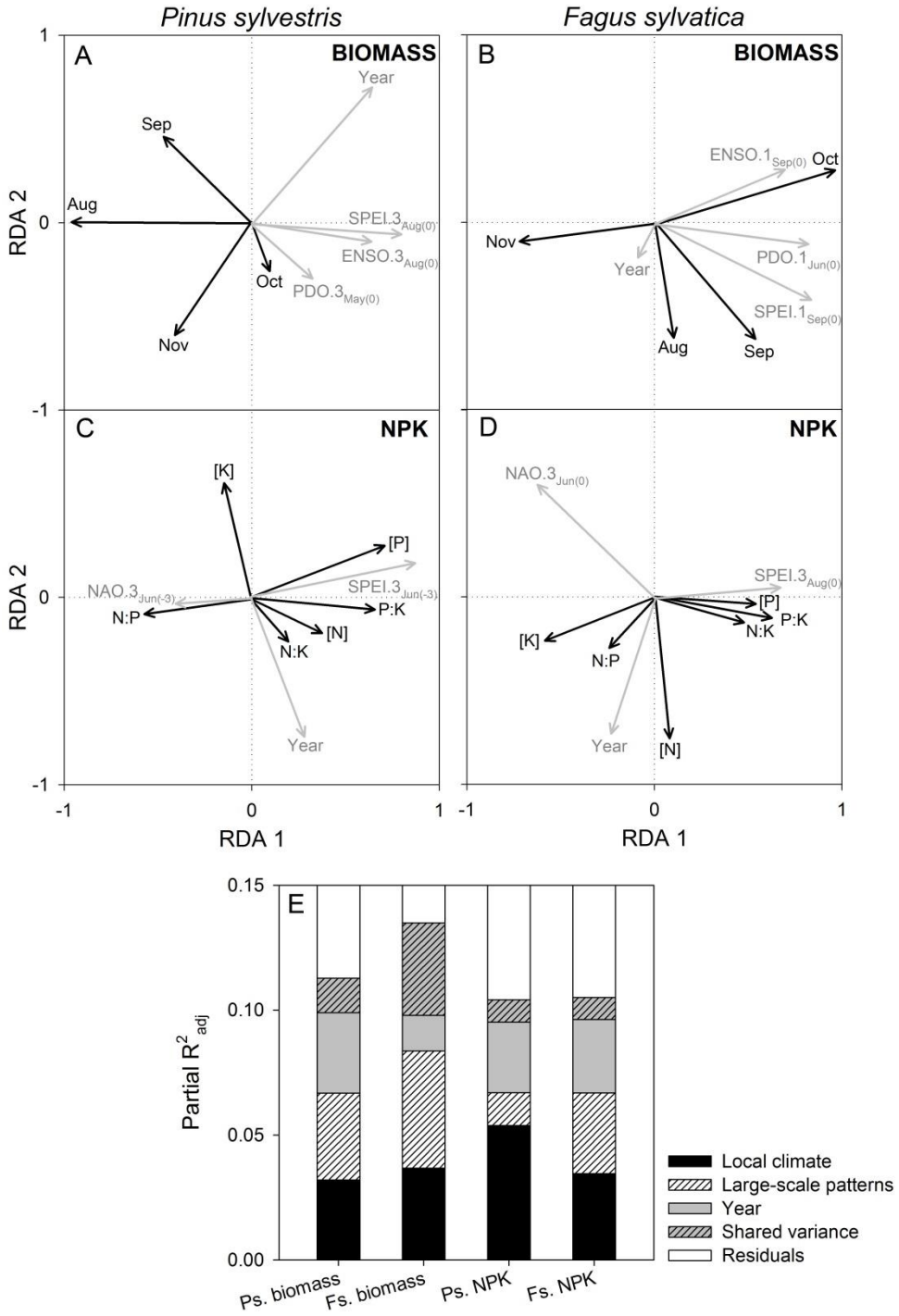

Figure 3. Redundancy analysis (RDA) based on experimental plots as cases, climate variables, and year as predictive matrix and response matrix of oscillatory components (OCs) of leaf litter monthly production ('Biomass') of Scots pine (*Pinus sylvestris*) (A) and European beech (*Fagus sylvatica*) (B), and OCs of concentrations of N, P and K and their stoichiometric relationships ('NPK') of Scots pine (C) and European beech (D). Both sites are analyzed together. Climate variables are represented as $INDEX.X_{Month(Y)}$ where X is the time scale in months, and Y is the time lag in years. Time lags represent maximum cross-correlations of climate variables with litter production and composition. Partial adjusted R^2 of local climate (SPEI), large-scale circulation indices (NAO, ENSO and PDO) and year, as well as the common fraction among them are also represented (E).

3.2. Linking leaf litter dynamics, TRW and iWUE of Scots pine

Figure 4A shows the relationship between timing of needle litter drop and tree-ring formation during the same year for Scots pine trees. PC1 explained 26.77 % of variance and established a connection between needles fallen in September and TRW, which was also reduced as trees got older. PC2 related August needle litter and iWUE and explained 20.63 % of data set variability. The higher the iWUE, the earlier the needle abscission.

Composition and stoichiometry of leaf litter 3-year lagged explained the greatest variability of both TRW and iWUE (results not shown). PC1, which explained 34.71 % of variance, encompasses most of the variability of Scots pine secondary growth. This axis established a relationship among N content, N:P and P:K ratios, TRW and year (Fig. 4B). The higher the N content and N:P ratio the lower the TRW; whereas the TRW-P:K ratio relationship was positive. PC2, which explained 20.3 % of variance, related P content and N:K ratio with iWUE. iWUE responded positively to P content of leaf litter, and negatively to N:K ratio (Fig. 4B).

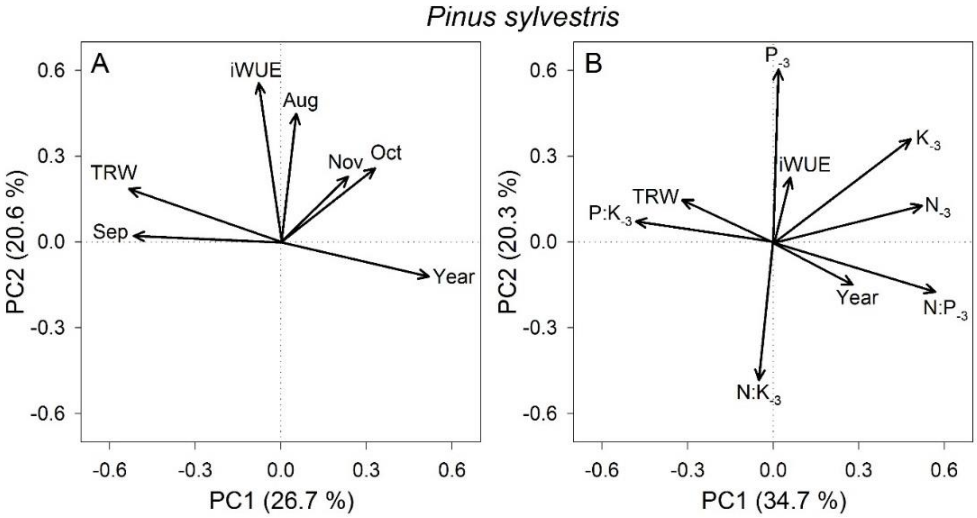

Figure 4. (A) Principal component analysis (PCA) based on experimental plots as cases with year, Scots pine (*Pinus sylvestris*) tree-ring width (TRW), intrinsic water-use efficiency (iWUE) and monthly leaf litter production of the same year than tree-ring formation (Aug, Sep, Oct, Nov). (B) PCA based on experimental plots as cases with year, TRW and iWUE of Scots pine, and nutrient contents (N_{-3}, P_{-3}, K_{-3}) and stoichiometry ($N:P_{-3}$, $N:K_{-3}$, $P:K_{-3}$) of overall leaf litter reaching forest floor three years prior tree-ring formation. Axes represent first and second principal components (PCs); in brackets the amount of explained variation by each PC is shown. Both sites are analyzed together.

3.3. Teleconnections of local climate and leaf litter dynamics

Significant correlations between atmospheric-oceanic oscillation indices and OCs of local climate variables were found for the period 1975 - 2015. $NAO_{February\text{-}March}$ exerted the greatest influence on maximum temperature from the same period at both Mediterranean (r = 0.691, p > 0.001) and continental (r = 0.698, p > 0.001) sites. Whereas autumn (October to December) minimum temperature showed positive correlations with $ENSO_{October}$ (MED site: r = 0.407, p = 0.008; CONT site: r = 0.516, p > 0.001) and $PDO_{October}$ (MED site: r = 0.525, p > 0.001; CONT site: r = 0.569, p > 0.001).

Precipitation displayed contrasting correlations with large-scale indices: negative with NAO during spring and positive with ENSO and PDO during summer. In the former case, NAO_{May} impacted precipitation from the same month (MED site: r = -0.583, p > 0.001; CONT site: r = -0.569, p = 0.002). On the other hand, August precipitation correlated with Pacific Ocean's circulation patterns from August at the Mediterranean site ($ENSO_{August}$: r = 0.647, p > 0.001; PDO_{August}: r = 0.481, p = 0.001), and from average July-August at the continental site ($ENSO_{July\text{-}August}$: r = 0.528, p > 0.001; $PDO_{July\text{-}August}$: r = 0.474, p = 0.002). Spatio-temporal correlations of local climate and gridded fields for the time period 1975 – 2015 were consistent with those found for large-scale circulation indices. Late winter-early spring maximum temperature was positively correlated with North Atlantic SLP (NAO influence area) and autumn minimum temperature with tropical and western Pacific Ocean SST (ENSO and PDO influence areas, respectively) (Figs. 5A and 5C). Spring and summer precipitation were negative and positively correlated with May North Atlantic SLP and summer Pacific Ocean SST, respectively (Figs. 5B and 5D).

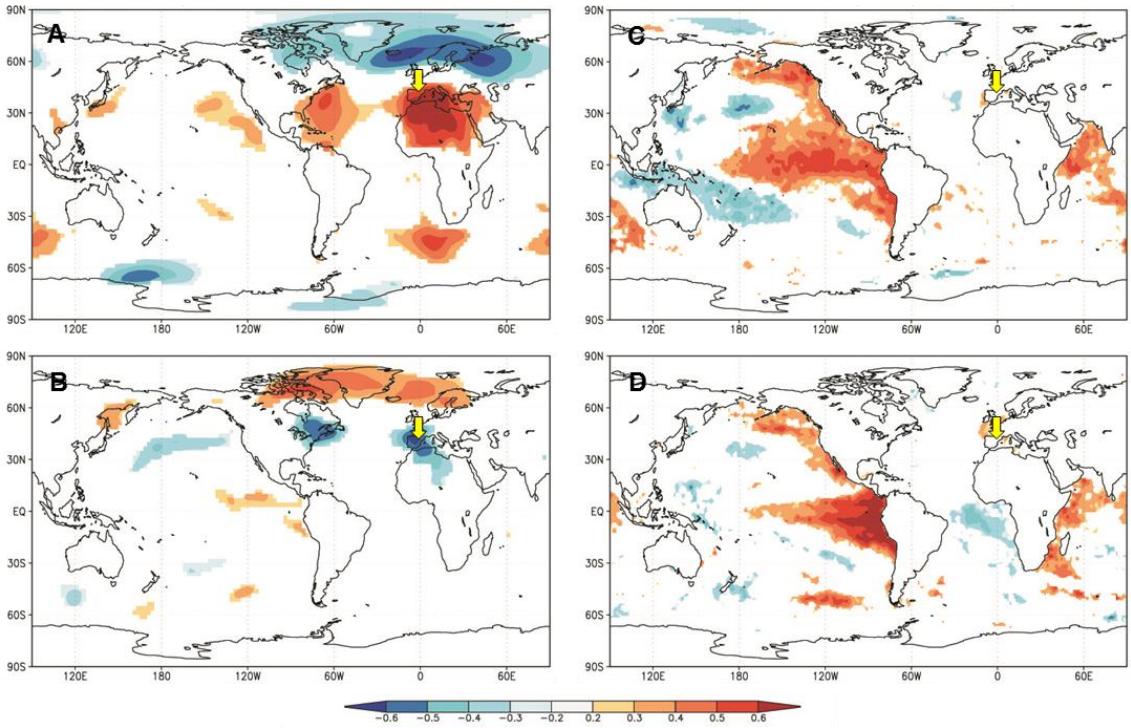

Figure 5. Spatiotemporal correlations between detrended NCEP/NCAR R1 sea level pressure (SLP, left) or detrended HadISST1 sea surface temperature (SST; right) and oscillatory components (OCs) of local climate datasets for the time period 1975 – 2015: (A) February to March SLP – February to March maximum temperature; (B) May SLP – May precipitation; (C) October to December SST – October to December minimum temperature; (D) August SST – August precipitation. Correlations with p < 0.1 are shown. Because of high similarities with the continental site correlation patterns, only correlations of local climate from the Mediterranean site are presented. Yellow arrows indicate location of the study sites.

The amount of explained variance of pine needle litter production by local climate equalled large-scale circulation patterns, whereas SPEI outperformed NAO explaining capacity in the case of needle composition. However, both beech leaf litter amount and composition were slightly better explained

by large-scales indices than by SPEI. Year also absorbed some variability of the data (Fig. 3E). ENSO and PDO presented higher correlations with monthly leaf litter production and NAO with leaf litter composition of both species (results not shown), so those large-scale circulation indices were included in the correspondent RDA analyses. A negative relationship was found between August and September needle litter fall and summer ENSO and spring PDO (Fig. 3A). $ENSO_{September}$ and PDO_{June} exerted a positive effect on the amount of beech leaf litter fall in October and negative on November beech litter (Fig. 3B). These patterns were reflected on the correlations found between leaf litter and tropical and western Pacific Ocean SST for the period 2000 – 2015 (Fig. 6). Late spring and early summer NAO of 3-year lagged positively affected N:P ratio of needle litter and negatively N:K and P:K (Fig. 3C). Although N:P of leaf beech litter did not show any clear response to spring and early summer NAO, N:K and P:K ratios did respond, with a negative correlation through the effect of NAO on soil moisture (Fig. 3D). As in the case of leaf litter biomass, strong spatiotemporal correlations calculated for the period 2000 – 2015 were found between stoichiometric relationships of leaf litter and SLP of the North Atlantic Ocean (Fig. 7).

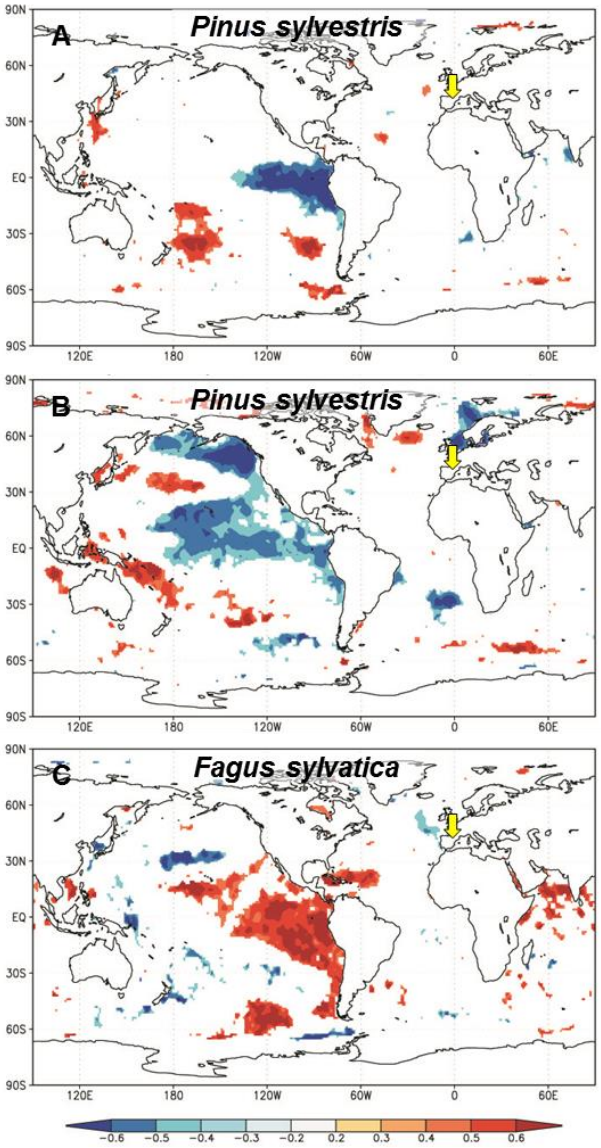

Figure 6. Spatiotemporal correlations between detrended HadISST1 sea surface temperature (SST) and oscillatory components (OCs) of leaf litter production for the time period 2000 – 2015: (A) June to August SST – August to September Scots pine needle production at the Mediterranean site; (B) August to October SST – August to October Scots pine needle production at the continental site; (C) September SST – September to October European beech leaf litter production at the Mediterranean site. Correlations with $p < 0.1$ are shown. Yellow arrows indicate location of the study sites.

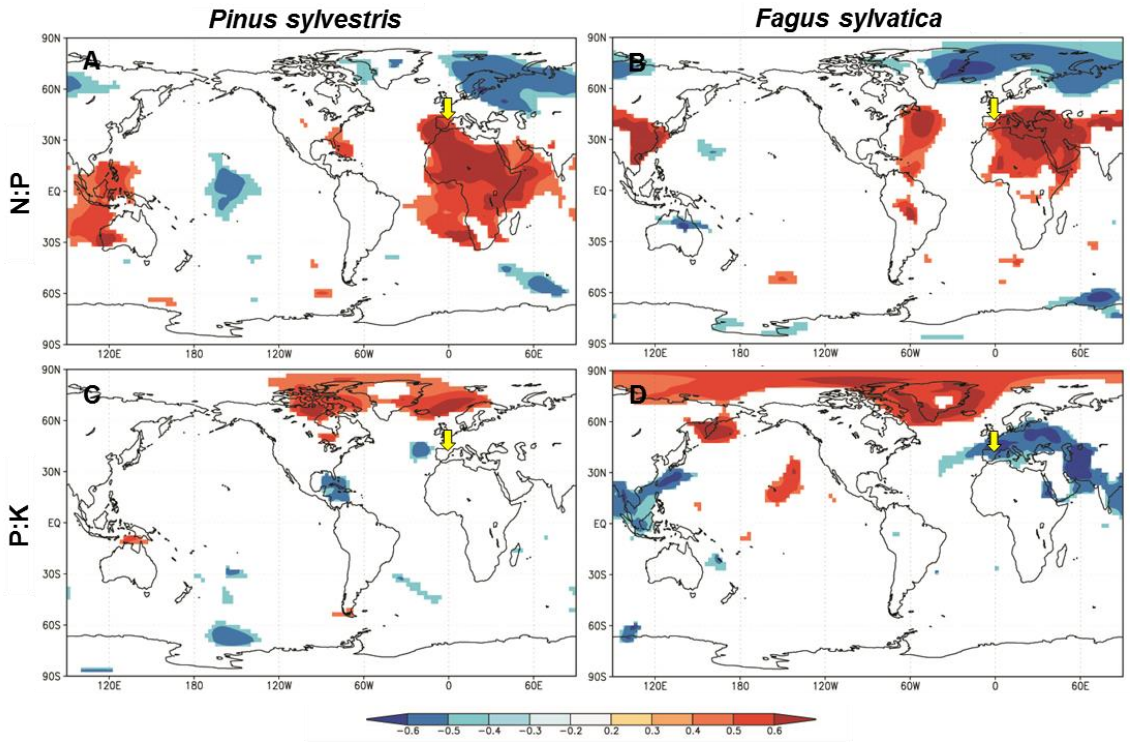

Figure 7. Spatiotemporal correlations between detrended NCEP/NCAR R1 sea level pressure (SLP) and oscillatory components (OCs) of leaf litter production for the time period 2000 – 2015: (A) 1-year lagged January SLP – Scots pine needle litter N:P ratio at the Mediterranean site; (B) current February SLP – European beech leaf litter N:P ratio at the Mediterranean site; (C) current April SLP – Scots pine needle litter P:K ratio at the continental site; (D) current March-May average SLP – European beech leaf litter P:K ratio at the continental site. Correlations with $p < 0.1$ are shown. Yellow arrows indicate location of the study sites.

4. DISCUSSION

Litterfall is the largest natural inflow of organic material and nutrients to the forest soils (Vitousek 1982). Tree species occupying the same site can differ conspicuously in nutrient return through litterfall (Reich et al. 2005). In mixed-species forests, the local effect of litter on soil properties depends on tree species involved and their relative contribution to the litter pool (Staelens et al. 2011), but direct extrapolations from their monospecific forests could not be accurate. Our first hypothesis was supported as a negative relationship was found between N:P ratio of leaf litter and growth of pine trees suggesting a possible P limitation of ecosystem processes such as decomposition. The second hypothesis of this study was also confirmed by the results since large-scale circulation patterns have a clear impact on leaf litter dynamics through ecosystem water availability. Leaf litter quantity had stronger response to changes in SST in the Pacific Ocean, whereas N:P:K stoichiometry showed stronger relationship with changes in SLP from the North Atlantic, possibly as a consequence of the different timings of influence of these large-scale patterns on local climate.

4.1. Influences of climate, site, and canopy composition on leaf litter production

The biggest fraction of aboveground litterfall corresponded to the leaves, which represented more than 70 % and 80 % in the Mediterranean and continental sites, respectively (Table 3). Consistently, leaf litter has been shown to be the most important litterfall fraction and the major determinant of nutrient cycling in forest communities owing to the high concentration of nutrients in leaves (Prescott 2002). These percentages were similar to those found in several mixed forests (Wang et al. 2008, Staelens et al. 2011). Blanco et al. (2006) collected litterfall every month during two years in the same experimental plots, showing that Scots pine needle litter production rates (MED site: *ca.* 3000 kg ha^{-1} yr^{-1}; CONT site: *ca.* 2800 kg ha^{-1} yr^{-1}) were in the upper edge of the range observed in Spain and more northern locations (Pausas 1997, Santa Regina & Tarazona 2001, Martínez-Alonso et al. 2007, Starr et al. 2005).

The reduction of needle fall in the Mediterranean site throughout the study period can be attributed to the increasing contribution of beech to total leaf litter (Fig. 1A). This increase is related to the expansion of beech crown cover over the plots during the last years, as already reported in a previous study in the same site (Primicia et al. 2013). At this site the replacement of pine trees by beech trees following the natural succession is progressively occurring as beech already exceeded pine in litter circulation by the end of the study period. However, the small magnitude of beech leaf litter at the continental site highlighted that the successional process towards a mixed canopy is still in a preliminary stage. Assuming a linear reduction of 3.4 % $year^{-1}$ in pine needle litter and an increase of 11.9 % $year^{-1}$ in beech leaf litter (based on the 16-year study period), beech litter would take *ca.* 30 years to surpass pine litter circulation at the continental site.

Climatic influence on litterfall dynamics could account for the seasonal variability of leaf fall within and between sites. As reported by Liu et al. (2004) for coniferous and broadleaf forests at Eurasian scale, we have found distinct climatic effects on pine and beech. On one hand, pine needle fall responded to soil water conditions during summer months, so that the drier the summer the earlier the needle shedding (Fig. 3A). Water stress prevents the tree from maintaining all its leaf biomass and accelerates the fall of the older needles (Reich & Borchert 1984, Wright & Cornejo 1990, Pausas 1997, Santa Regina & Tarazona 2001, Martínez-Alonso et al. 2007) as a result of the increase of abscisic acid levels (Sundarapandian & Swamy 1999). Several authors have reported this dependence between water availability and litterfall for pine species (Pausas et al. 1994, Pausas 1997, Berg & Meentemeyer 2001, Blanco et al. 2006, Martínez-Alonso et al. 2007), although other studies have found opposite results when there was no water limitation (Starr et al. 2005, Lehtonen et al. 2008). Consistently, the earlier needle fall peak in the Mediterranean site (August-September) compared to the continental site (September-October) was probably the result of greater water stress and higher temperatures during the summer period in the former site. On the other hand, abscission of beech leaves before the main peak as a consequence of high water availability in September (Fig. 3B) may seem contradictory according to the afore-mentioned explanation. However, it should be understood in terms of the physical impact exerted by precipitation that can remove old and senescent leaves from the canopy. Consistently, frequent heavy rains and storm activity during autumn after the end of dry season have

been reported in the Mediterranean region (Romero et al. 1998) where an increase in heavy precipitation events is expected (IPCC 2013).

4.2. Leaf litter nutrition: a proxy of ecosystem nutrient limitation

The nutrient status of leaf litter is primarily the product of the nutrient status of green leaves and the ratio of nutrient resorption (Killingbeck 1996, Kobe et al. 2005). Nutrient concentrations in green leaves vary widely among different species, and such differences increase with phylogenetic distance (Sardans et al. 2015). Analogous differences in senescent leaves were found when different functional groups (e.g. coniferous vs. broadleaf) were compared (Kavvadias et al. 2001, Cornwell et al. 2008). Likewise, we have found outstanding differences between Scots pine and European beech as concentrations of all macronutrients analyzed in this study (N, P and K) were higher in beech leaf litter than in pine needles (Fig. 2). It has been suggested that evergreen species reduce nutrient losses by the synthesis of leaves with low nutrient concentrations and long life spans (Escudero et al. 1992, Aerts 1996), whereas high nutrient concentration in beech leaves has been associated with an enhancement of subsequent nutrient acquisition from soil by beech trees (Meier et al. 2005).

Besides between-species differences, nutrient composition and stoichiometry significantly differed between the two study sites (Table 4), suggesting the existence of other factors affecting leaf litter composition. Earlier studies have shown that both green leaves nutrients (e.g. Reich & Oleksyn 2004, Sardans et al. 2013) and its resorption in trees (e.g. Aerts 1996, Killingbeck 1996, Blanco et al. 2009, Primicia et al. 2014) are related to climatic factors. Therefore, leaf litter nutrients are expected to be climate-dependent. Indeed, global patterns of leaf litter nutrient variation at regional (Aerts 1007, Liu et al. 2006) and global scale (Aerts 1997, McGroddy et al. 2004, Yuan & Chen 2009, Kang et al. 2010) have been identified. Although those studies suggest that globally temperature is the most important climatic factor controlling leaf litter composition, in water-limited ecosystems, such as the Mediterranean ones, water availability may play a key role. Accordingly, we have found that SPEI accounted for some year-to-year variability (Fig. 3C and D). The observed maximum cross-correlations between SPEI and nutrient composition at long-term lag (3 years) for pine could indicate that senescent needle composition is related to climate at the time of needle production as needles in the study stands have 3-5 years life span (Blanco et al. 2009, Primicia et al. 2014).

Water availability showed a positive relationship with [P] in both species and [N] in the case of pine. Drought may decrease nutrient mineralization (Cornwell et al. 2008, Zhang et al. 2008) and nutrient mobilization from the soil (Sardans & Peñuelas 2007, Yuan & Chen 2015a), which can reduce nutrient uptake and allocation to leaves (Sardans et al. 2012a, 2012b, Kreuzwieser & Gessler 2010). Water availability has been also reported to modify nutrient resorption efficiencies (del Arco et al. 1991, Yuan & Chen 2009b). However, our data set based on leaf litter nutrients does not allow us to disentangle the relative importance of each of those processes. Additionally, climate effects are difficult to isolate from the influence of soil fertility and other site-specific factors on green leaves nutrients and resorption. In any case, we have found clear matches between leaf litter and soil in N (MED site > CONT site) and P (MED site < CONT site) concentrations, which is consistent with previous studies conducted in pine and beech forests (Vesterdal 1999, Kavvadias et al. 2001). N:P ratios were

found to negatively respond to water availability. The N:P ratio response to drought agrees with previous results from green leaves (Sardans et al. 2011, Sardans et al. 2013). Furthermore, the N:P ratios insenescent pine needles higher than those in green needles (see Blanco et al. 2009 and Primicia et al. 2014) indicate than pine trees resorb more P than N during senescence, as it is predicted to occur in P-limited ecosystems (McGroddy et al. 2004).

Meanwhile, [K] was negatively related to SPEI in beech leaf litter. K represents a particular case as it is highly mobile and can be increasingly leached away with higher rainfall, which agrees with the lower [K] at the continental site (Table 4). Furthermore, K is particularly important in dry environments since this element plays a role in controlling leaf water loss as it boosts stomatal function (Khosravifar et al. 2008), the control of osmosis (Babita et al. 2010), and the hydraulic conductance of water (Oddo et al. 2011). In summer, K is allocated to leaves in order to avoid water stress (Sardans et al. 2012a), so leaf litter could easily reflect such mechanism since leaf shedding occurs in late summer and autumn. This assumption finds support in the higher [K] in beech leaves at the sub-xeric Mediterranean site (Fig. 2C), and in the negative relationship between [K] and summer SPEI found only in beech leaf litter (Fig. 3D) –in accord with high sensitivity to drought of beech (Geßler et al. 2007) - since greater K allocation to leaves is expected under drier conditions. As might be expected, SPEI was also associated with N:K and P:K ratios of both species (Fig. 3C and D). Likewise, Gotelli et al. (2008) have reported that N:K concentration ratios in plants correlate with the water content of soils. Drought has been found to decrease contents of N and P in aboveground biomass but did not change K contents, which has been associated to differences in nutrient solubility among elements (Sardans & Peñuelas 2007).

Nutrient concentrations and their stoichiometric relationships in leaf litter can determine the rate of decomposition and nutrient release, and therefore their subsequent availability for other plants and soil organisms (Berg & McClaugherty 2003, Mooshammer et al. 2012). Hence, leaf litter nutrient status may inform about nutrient limitation at ecosystem level (Reed et al. 2012, Lang et al. 2016). The identification of critical leaf litter elemental stoichiometry ratios from which microbial decomposition is limited by N or P has been attempted in several studies (Aerts 1997, Smith 2002, Güsewell & Freeman 2005, Mooshammer et al. 2012). Güsewell & Freeman (2005) found that decomposition was always P-limited for litter with N:P ratio above 22. Considering such threshold we could state that decomposition of leaf litter of both Scots pine and European beech is limited by P at the Mediterranean site (Fig. 2D). Although litter N:P was lower than 22 at the continental site, P was immobilized for at least 5 years, while some net mineralization of N occurred during that period (Blanco et al. 2011), suggesting than P could also be limiting decomposition rate. Regardless of specific values, decomposition rates have been negatively associated with N:P ratios of leaf litter (Schneider et al. 2012). Hence, the increasing patterns of N:P ratios of both species at both sites could result in slowing down the P mineralization rate, thus reducing P availability for trees. P immobilization by soil microbes has been observed in P-depleted soils, where belowground microbial biomass contains the major proportion of P-pools (Vincent et al. 2013). Consistently, Blanco et al. (2009, 2011) and Primicia et al. (2014) have already proposed that the same experimental forests may be P-limited based on foliar nutrition, resorption, and decomposition information. This situation could lead to a deterioration of P nutrition, as has been reported for Central European forests of Scots pine (Prietzel

et al. 2008, Jonard et al. 2015) and European beech (Braun et al 2010, Jonard et al. 2015, Talkner et al. 2015, Hofmann et al. 2016).

The global pattern of increasing N inputs to forest ecosystems (Galloway et al. 2004) has been also reported for the last decades in NE Spain (Ávila & Rodá 2012). Indeed, Pyrenean forests have been identified as one of the ecosystems with a higher saturation risk due to N deposition, mainly coming from cross-border sources (García-Gómez et al. 2014). Accordingly, a situation close to N saturation in pine-beech mixtures of the Pyrenees has been proposed using a modeling approach (Blanco et al. 2017). Increased N inputs can reduce P availability because of the N fertilization effect that increases the demand for other nutrients such as P (Peñuelas et al. 2012), the reduction in fine root biomass, which negatively affects the development of mycorrhiza and induces changes in the microbial community structure (Waldrop et al. 2004, Kjøller et al. 2012), or increased phosphate adsorption due the acidifying effect of N (Geelhoed et al. 1997). Besides, increased N availability is expected to modify recycling strategies by trees, and thus litterfall N:P ratios are expected to increase as a result of a decrease in N resorption (Zechmeister-Boltenstern et al. 2015). Consequently, the role of P limitation in soil trophic webs is increasing and natural and managed ecosystems are gradually moving from N to P limitation (Peñuelas et al. 2013). In addition, the arise of a co-limitation by N and P in Pyrenean pine-beech mixtures could result in a higher sensitivity to other environmental stresses such as droughts or pests, which may prompt a rise in tree mortality (Braun et al. 2010, Blanco et al. 2012).

Furthermore, mineralization of nutrients is often limited by low C quality as a significant fraction of essential nutrients, mainly N, are bound to recalcitrant lignin-like compounds (Zechmeister-Boltenstern et al. 2015). The increasing contribution of European beech to forest leaf litter leading to the development of mixed stands over the last decades (Fig. 1A), particularly at the Mediterranean site, has major implications for turnover rates and nutrient cycling in the ecosystem. Deciduous leaf litter generally has lower lignin and polyphenol concentrations than conifer litter, so it would be expected to decompose faster (Perry et al. 1987) and even hasten the decomposition of needle litter (Polyakova & Billor 2007). Niinemets & Tamm (2005) stated that mixed-species forest communities appear to produce litters with chemical composition varying more widely than pure stands, and that mixed litters may support a more diverse soil microfauna and microbial populations. Besides to the direct effect of species-specific litter traits, tree species richness and composition has been shown to modify decomposition indirectly through changes in micro-environmental conditions (Joly et al. 2017).

4.3. Connections among leaf litter dynamics and Scots pine radial growth and iWUE

Although researchers have tried to connect leaf litter production with tree growth, results remain inconclusive. Different authors did not detect such relationship from short litterfall series (Wirth et al. 2002, Martínez-Alonso et al. 2007). A weak correlation between productivity and litterfall was reported by Lehtonen et al. (2008) from a long-term study (43 years) in a Scots pine forest in Finland. In this study, we have found that timing of Scots pine needle litter influenced TRW, in such a way that the more needles fell in September, the more pine trees grew (Fig. 4A). Needle shedding prior to September was linked with water stress during summer (see section 4.1.), which has also been

frequently associated with growth reductions in Mediterranean Scots pine populations (*e.g.* Martínez-Vilalta et al. 2008, Primicia et al. 2013). Both Primicia et al. (2013) and Cardil et al. (2018) have reported a secondary growing peak of Scots pine in October for which the maintenance of green needles longer before senescence may play a key role. Further, seasonality of needle litter production was found to be linked with iWUE of trees through the effect of water availability (Fig.8). Summer water stress may have involved a premature needle shedding during August, which finally results in formation of tree-rings with greater iWUE (Fig. 4A). The effect of air humidity or soil moisture on iWUE has been widely reported (e.g. Waterhouse et al. 2004, Linares & Camarero 2012, González de Andrés et al. 2018).

The productivity of forests is highly dependent on soil nutrient availability, which is determined in part by leaf litter composition and stoichiometry. Leaf litter quality has indirect effects on water use and growth of trees through several ecosystem processes, such as nutrient mineralization, uptake and allocation to different tree organs. As mentioned above, rates of decomposition and mineralization are strongly influenced by litter quality. Following the consumer-driven nutrient recycling theory (Sterner & Elser 2002), we assumed that leaf litter stoichiometry influences the rate at which each nutrient becomes available for tree uptake. Supporting this assumption, we have found a negative relationship between TRW and N:P ratio of leaf litter fallen three years prior tree-ring formation (Fig. 4B), which is in concordance with the P-limited decomposition previously reported (see section *4.2.*). This result should be cautiously interpreted as net P release has not been observed after 3 years of decomposition neither for pine needles (Blanco et al. 2011) nor for beech leaves (unpublished results). Instead, high N:P ratios may negatively affect growth rate of soil microbes (consistent with the growth rate hypothesis, Sterner & Elser 2002), and thus reduce rate of leaf litter decomposition (Fig. 8).

Scots pine iWUE also responded to stoichiometry of leaf litter fallen with a 3-year time lag, showing a negative relationship with N:K ratios (Fig. 4B). This result highlights the role of K in tree physiology, as it is involved in the enhancement of iWUE, preventing embolism of the xylem and reducing water loss (Trifilo et al. 2008, Sardans et al. 2012a). Recent studies have evidenced the important role of K content and its stoichiometric relationships for water stress resistance in the Mediterranean region (Sardans & Peñuelas 2007, Sardans et al. 2012a, Sardans et al. 2013). Therefore, K should be included in ecological stoichiometric studies because additionally it is an important component of plants, K concentrations in leaves are often higher than P concentrations, it is a key element to adjust cellular osmosis, and its role in controlling stomata and water-use efficiency (Egilla et al. 2005, Babita et al. 2010, Sardans et al. 2012a).

4.4. Large-scale circulation patterns impacts on leaf litter dynamics

Our results show that natural SLP variability of the North Atlantic Ocean had significant correlations with local climate variables from the western Pyrenees (Fig. 5A & 5B). The NAO is the most important source of climate variability in Europe (Hurrel 1995). It has a strong effect on winter/spring climate over the Iberian Peninsula (Hurrel & Van Loon 1997, Rodó et al. 1997, Osborn 2011). We have also detected a significant effect of North Atlantic pressure variability on winter and spring maximum temperature (Castro-Díez et al. 2002). However, climate and hydrological conditions in the Pyrenees are not only influenced by NAO, but also by other atmospheric dynamics originated in the Pacific Ocean that operate at long distances, such as ENSO and PDO (Rodó et al. 1997, Pozo-Vazquez et al. 2005, Gámiz-Fortis et al. 2011). On one side, ENSO represents the strongest interannual variation of Earth's climate (Stenseth et al. 2003) that influences the climate of both tropical and extratropical regions (Gámiz-Fortis et al. 2011). Consistent with our results (Fig. 5D), precipitation in the Iberian Peninsula has been shown to increase during late summer, autumn, and early winter when El Niño conditions are present in the Pacific (Pozo-Vázquez et al. 2005, Shaman & Tziperman 2011). On the other side, a recent study has pointed out that PDO modulates the effect of ENSO, so that when in phase with the PDO, ENSO-induced dry–wet changes are magnified (Wang et al. 2014). This fact is supported by our results since PDO and ENSO do work in the same direction both for local climate variables (Fig. 5C & 5D).

Leaf litter dynamics of forest ecosystems may not reflect only local climate variations, but also large-scale atmospheric-oceanic circulations, which can provide a broad understanding of observed changes in the local physical environment and the associated ecological processes (Stenseth et al. 2002, 2003, Hallet et al. 2004). We have found that seasonality and chemical composition of leaf litter were influenced by different large-scale oscillations. Indeed, the amount of variance explained by large-scale climatic indices was higher than that by local climate in the case of monthly leaf litter production and similar when nutrient composition was analyzed (Fig. 3E). These associations can be understood through the afore-mentioned impact of water availability on litterfall as atmospheric-oceanic circulations exert their influences on ecological systems through local weather variations (Stenseth et al. 2003).

Firstly, ENSO has been shown to be the most influential large-scale climate pattern in leaf shedding timing of both species (Fig. 6). A positive phase of ENSO during late spring and summer brings higher precipitation so pine trees retain needles for a longer time. In the case of beech leaves, whose fall is advanced by heavy rain during September, there has been found a teleconnection with September ENSO closely linking storm activity during fall and winter in Western Europe (Shaman 2014). Secondly, stoichiometric ratios of leaf litter were mainly affected by NAO during winter and spring (Fig. 7). When in its positive phase, NAO may have caused drier conditions during the growing season, so enhancing N:P ratios and diminishing K-related stoichiometric relationships. The fact that features of leaf litter were mainly affected by different large-scale climatic indices may be related to the timing when these patterns exert their influence on local climate. That is, production and seasonality of leaf litter have been found to be more affected by summer and early autumn conditions, when ENSO exerts its maximum impact; whereas NAO's influence was described earlier in the growing season so driving patterns of nutrient composition. Therefore, the results suggest complex leaf litter dynamics regulated by global atmospheric-oceanic patterns, in which leaf abscission seasonality

would be mainly affected by Pacific Ocean SST and leaf litter stoichiometry, and thus ecosystem nutrient limitations, by pressure differences in the North Atlantic Ocean. Figure 8 summarizes the linkages among large-scale circulations and local climate variables, and their further impacts on seasonality and stoichiometry of leaf litter and tree-ring information of Scots pine.

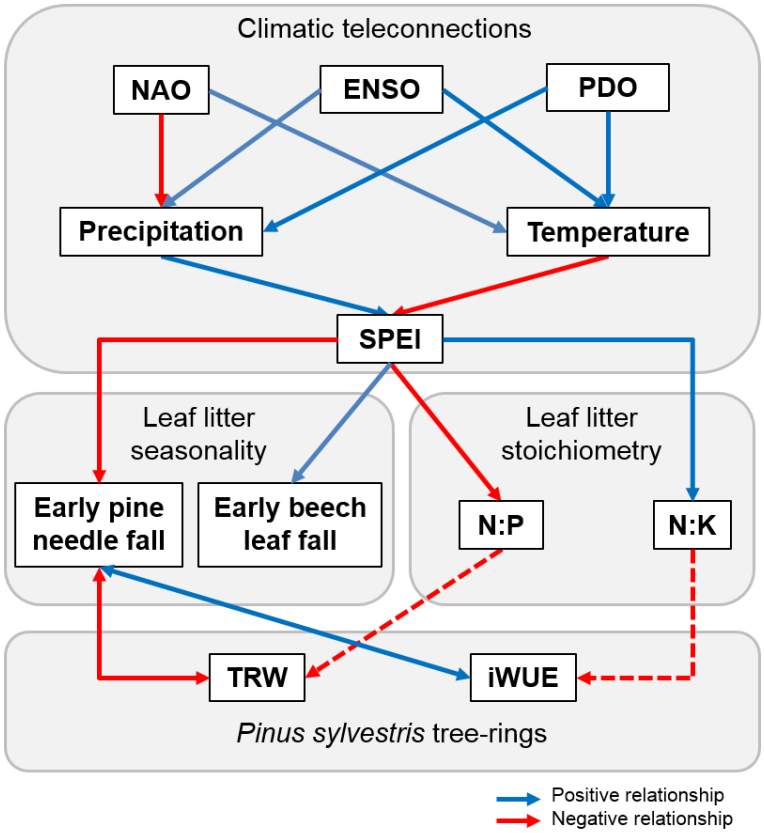

Figure 8. Conceptual framework linking large-scale oceanic-atmospheric circulation patterns (North Atlantic Oscillation, NAO; El Niño – Southern Oscillation, ENSO; and the Pacific Decadal Oscillation, PDO), local climatic conditions (Precipitation, Temperature, and standardized precipitation evaporation index, SPEI), timing of leaf litter abscission and stoichiometric relationships (N:P and N:K) of Scots pine (*Pinus sylvestris*) and European beech (*Fagus sylavtica*). In the case of Scots pine tree-ring width (TRW) and intrinsic water-use efficiency (iWUE) are related to leaf litter seasonality and stoichiometry. Blue and red lines represent positive and negative relationships, respectively. Dash lines represent an indirect relationship through decomposition and nutrient release processes with a time lag of 3 years between leaf fall and tree-ring formation of pine trees.

5. CONCLUSIONS

Long-term studies of litterfall dynamics are important in order to reach a better understanding of energy and nutrients transfers from trees to soil in forest ecosystems. Leaf litter constituted the biggest fraction of litterfall production in mixed forest of Scots pine and European beech stands located close to the southwestern edge of species distribution. Along the 16-year period, European beech crown cover has expanded in formerly Scots pine-dominated stands, which may have important effects on forest functioning considering seasonal and compositional differences between leaf litters of both species. Large-scale atmospheric-oceanic oscillations account for major variations in water availability in the Pyrenees, which has been found to play an important role in pine-beech stands in both leaf shedding seasonality – mainly influenced by ENSO – and nutrient return to forest floor – which primarily reflects the impact of NAO –. Summer droughts hastened pine needle fall during late summer and autumn, whereas early autumn storms produced premature abscission of beech leaves. Soil water condition also affected nutrient availability, which in turn apparently modified nutrient uptake, resorption efficiency, and nutrient allocation to leaves and therefore leaf litter nutrition.

Increasing trends of N:P ratios in leaf litter of both species particularly at the Mediterranean site pointed out an increasing P limitation in Pyrenean Scots pine – beech mixtures at our study sites. Leaf litter seasonality was related with growth and water-use efficiency of Scots pine as premature needle abscission due to drought enhanced iWUE and reduced TRW. Furthermore, stoichiometry of leaf litter influenced pine TRW and iWUE with a 3-year lag probably through its effect on decomposition and nutrient release rates. The strong interconnections among climatic conditions at global and local scales, leaf litter dynamics and tree performance (i.e. secondary growth and iWUE) have been summarized in a conceptual model (Fig. 8) that constitutes a novel contribution to knowledge of mixed forest ecosystem functioning.

The predicted changes of NAO towards more positive phases and the intensification of ENSO-induced rainfall variability due to changes in moisture availability (Christensen et al. 2013) may enhance the frequency and severity of droughts in the Pyrenees (IPCC 2013). Considering the correlation between water availability and leaf litter dynamics in Scots pine – European beech mixtures in their distribution edges, decreases in decomposition and nutrient release and deterioration in trees nutrition might be expected. Hence, direct effects of water shortage would be worsened in drought-prone environments, such as circum-Mediterranean regions, by reducing capacity of trees to use water efficiently and the consequent decrease in growth and carbon storage capacity.

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GENERAL DISCUSSION

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Since 1999 two mixed forests located in the southwestern Pyrenees, northern Spain (province of Navarre), have been monitored providing information about important forest processes, such as decomposition, nutrient resorption, nutrient mineralization, nutrient return through litterfall, microclimatic conditions, etc. and their influence on forest productivity (e.g. Blanco et al. 2006, 2008, 2009, 2011, Primicia et al. 2013, 2014, Candel-Pérez et al. 2108, Cardil et al. 2018). During the time of monitoring these sites, a gradual shift has been observed in the structure and functioning of the forests. This is a common process already observed in Europe, where over recent decades European beech (*Fagus sylvatica* L.) growth under Scots pine (*Pinus sylvestris* L.) canopy has progressively resulted in mixed stands. Although mixed-species forests have been identified as an adaptation strategy in forest management in the face of climate change due to increased productivity compared to pure stands (Zhang et al. 2012, Vilà et al. 2013, Liang et al. 2016) and stabilizing effects (Jucker et al. 2014, Metz et al. 2016, Río et al. 2017), there are still many gaps in the knowledge of mixtures responses to shifts in environmental conditions. Consequently, a set of experimental plots were established in two forest stands of contrasting climatic and fertility characteristics: a sub-xeric site located at low elevation with a cool and wet Mediterranean climate and high productive (Aspurz), and a mesic site situated at high elevation characterized by cold-wet continental climate and with low productivity (Garde). In this context, this thesis research has been focused on the effect of species interactions on cycling of nutrients and tree physiology and productivity, in terms of aboveground biomass, secondary growth and litterfall characteristics. Special attention has been paid to the influence of water availability as in the context of global change the frequency and intensity of droughts are predicted to increase in the Mediterranean region (IPCC 2013).

Climate is one of the main environmental factors determining forest structure and function, and water availability has been found to be a major limiting factor on forest productivity. However, tree growth is a multi-faceted biological process that can depend simultaneously on several interacting factors besides climate. In agreement with previous studies (e.g. Primicia et al. 2013, Fernández-de-Uña et al. 2016, Forrester et al. 2016, Metz et al. 2016), we have found that interspecific interactions in mixed-species forests greatly modify stand- and species-level responses to environmental factors at our study sites (González de Andrés et al. 2017, 2018), and thus they should be considered when designing management plans.

Pyrenean Scots pine – European beech mixed forests are located close to the limit of species distribution and therefore are of great interest because they portray ecological scenarios which can develop in more northern areas under warmer or drier conditions (Hampe & Petit 2005). Besides, this region is likely to be highly sensitive to environmental shifts so the changes caused by climate change will be noticeable earlier than in core distribution areas (Castro et al. 2004). Different methodologies have been used to evaluate mixing effects on functioning of these mixtures, including tree-ring information about secondary growth and their C isotope ratio ($^{12}C/^{13}C$) from 34-year series (Chapter 1, hereafter referred as González de Andrés et al. 2018) and a modelling approach with the process-based, ecosystem-level model FORECAST Climate (Chapter 2, hereafter referred as González de Andrés et al. 2017).

The growth response of Scots pine to increasing levels of interspecific competition was opposite in the two study sites: negative at the Mediterranean site and positive at the continental site (González de Andrés et al. 2018). This finding can be explained following the hypothesis that mixing effects on Scots pine were due to light-related interactions. Complementary traits regarding morphology and size distribution of crowns of both species have been proposed to result in mixtures with a multi-layered canopy (Jucker et al. 2015, Pretzsch et al. 2015, 2016), which exhibit a proportion of vertical leaf area overlap in mixtures lower than expected (Forrester et al. 2018), and temporal separation of light absorption due to the deciduousness of European beech (Ishii & Asano 2010, Lu et al. 2016). Besides, Pretzsch et al. (2016) have described synergistic mixing effects at structural levels since increased morphological variability and crown extension were observed in mixtures compared with pure stands. The same study also found higher interlocking and canopy space filling in the lower canopy layers likely owing to the contrasting light compensation points and light-use efficiencies of both species (Pretzsch et al. 2016). As a consequence, increased light absorption of Scots pine that correlates with the mixing effect on pine growth has been reported when European beech is admixed (Forrester et al. 2018). In addition, the admixture of European beech may improve nutrient supply for Scots pine due to the higher quality of beech leaf litter (Chapter 3) with higher decomposition rates (Rothe & Binkley 2001) that may even hasten decomposition of pine needle litter (Polyakova & Billor 2007). Simulations with FORECAST Climate confirmed that the mixing effects found at tree-neighbourhood level are maintained also at stand level and the assumption of light-related mixing effects on Scots pine at even longer time scales. Larger crowns of Scots pine trees with higher N contents were predicted in mixed stands compared with pure stands by model simulations, thus leading to enhanced light absorption and complementarity effects on pine growth (González de Andrés et al. 2017). It is noteworthy that in the Chapter 3 we described changes in nutrient concentrations and stoichiometry of leaf litter along the last 16 years, suggesting an increase in P limitation of decomposition and nutrient release processes, which may lead to an alteration of nutrient cycling at ecosystem level. There might be implications for the facilitative effect of beech litter on Scots pine if the same tendencies of nutrient composition of leaf litter are maintained or intensified.

However, the strength of mixing effects regarding structural heterogeneity has been shown to be enhanced as water availability increases (Forrester & Albrecht 2014, Condés & Río 2015, Pretzsch et al. 2016). Likewise, our results showed that Scots pine is subjected to net interspecific competition with European beech in the drought-prone Mediterranean site. Light-related mixing effects on Scots pine appear to be overridden by competition for water resources with European beech under drier conditions, what is also suggested by the increase of iWUE of pines under high interspecific competition (González de Andrés et al. 2018). Indeed, drought resistance in mixed forests has been found to be not always positively correlated with species richness (Grossiord et al. 2014a, Forrester et al. 2016, Metz et al. 2016). Physiological and ecological traits of the mixed species coupled with edaphic and other site characteristics should be considered instead. Therefore, frequent summer droughts at the Mediterranean site in combination with faster depletion of soil water and higher canopy interception of rainfall in mixtures (Primicia 2012, Grossiord et al. 2014b, Cardil et al. 2018) could be responsible for cancelling out light-related mixing effects on Scots pine, which is outcompeted by European beech. In agreement, other studies analyzing intra- and inter-annual growth dynamics of

both species have reported growth reductions of Scots pine growing under mixed canopies at the same experimental plots (Primicia et al. 2013, Cardil et al, 2018) and in other Pyrenean forests (Río et al. 2014a). Indeed, Cardil et al. (2018) found that growth differences between pure and mixed canopies were significant at low and medium throughfall. Likewise, our simulation approach supports an increasing competition for water in mixtures as climate becomes drier. When climate change scenarios were simulated biomass accumulation after a 150-year period of stand development is reduced at the Mediterranean site (- 33 %) and increased at the continental site (+ 11 %) compared with historical climate (González de Andrés et al. 2017). Such values should be taken with caution due to the lack of site-specific validation of FORECAST Climate in the study forests. However, both basic FORECAST and FORECAST Climate have been validated in different forest types covering six different biomes (see Appendix B Table S2) showing that the model is able to properly simulate forest functioning across a wide range of conditions. Therefore, the predictions in González de Andrés et al. (2017) enable us to get a glimpse of expected behaviour of pine-beech mixtures growing under harsher climatic conditions.

Differences between dendrochronological results and FORECAST Climate simulations – the latter predicted complementarity instead of competition on Scots pine at the Mediterranean site – might have several methodological explanations. Firstly, the time frame considered lasted a few decades from juvenile to mature stages in the dendrochronological approach but the whole life span of stands in the modelling approach. Secondly, although forest models are valuable tools for evaluating long-term effects of shifts in environmental conditions and management practices on forest functioning, they still constitute simplified representations of actual forest processes. Even calibrating FORECAST Climate with data from the experimental sites, the simulations are not accounting for other site-specific factors, such as the topography (e.g. distance to the river, slope, orientation), complex soil layers, neighbour effects or presence of tree species other than Scots pine or European beech, that although minor in biomass could be working as added biodiversity in plant and microbial communities. Furthermore, the only limiting nutrient included in the simulations was N, but there is increasing evidence of co-limitation of N and P in European forests (Braun et al. 2010, Jonard et al. 2015, Talkner et al. 2015, Hofmann et al. 2016), and at the study stands (Blanco et al. 2011, Primicia et al. 2014) in agreement with the results of Chapter 3. This chapter also highlighted that leaf litter composition, and resultant nutrient supply to forest soils, depends on water availability and established a connection between water and nutrient limitation. However, the complex interactions among limitations imposed by different resources make them very difficult to incorporate into ecological models. In any case, FORECAST Climate does not simulate interactions among species by using competition indices, but it includes explicit representations of competition for available resources among species cohorts that can vary along spatial and temporal gradients (Kimmins et al. 1999, Seely et al. 2015), which is considered a more suitable way to simulate mixing effects (Blanco et al. 2015, Pretzsch et al. 2015b).

Special attention should be paid to the procedures by which complementarity was assessed in the two different approaches. Finding pure reference stands can be difficult in some regions (Charru et al. 2012, Dirnberger et al. 2017). That is the case in our study region, where there is a lack of pure Scots pine or European beech stands and only small patches can be classified as pure canopy patches

(see the procedure followed in Primicia et al. 2013, 2014 and Cardil et al. 2018). Consequently, in the field-based dendrochronological study, complementarity was evaluated as the tree growth response to different values of interspecific competition by calculating a spatial competition index for each sampled tree (González de Andrés et al. 2018). Alternatively, comparisons of stemwood yield between pure and mixed stands were conducted in González de Andrés et al. (2017), following the common approach when addressing mixing effects on productivity (following Kelty 1992). Such complementarity definition has been shown to be very sensitive to the method used for species proportion estimation (Dirnberger & Sterba 2014, Sterba et al. 2014). It has been suggested that an appropriate species proportion calculation should consider the potential density of that species growing in a fully stocked pure stand, and such density needs to take climatic conditions into account (Dirnberger et al. 2017). We have fulfilled that condition since we have addressed species proportion by referring to the simulated density of pure stands at each of the two sites. In addition, different species do not have the same potential for volume growth, and thus to estimate species proportion we need to consider species differences in growing space requirements (Dirnberger & Sterba 2014). Instead, we have used stem number due to limitations of model outputs, which are based on a mass balance approach. Basal area or volume outputs of FORECAST Climate have not be validated for the study forests. Therefore, such estimation may have introduced some biases on the interpretation of mixing effects. Another possibility would have been using foliar N because is the driver of growth in FORECAST Climate (Kimmins et al. 1999) and could inform about light environment as a surrogate for crown space of species.

On the other hand, the growth response of European beech suggests a reduction of intraspecific competition when Scots pine is admixed (González de Andrés et al. 2017, 2018), which is consistent with previous results reporting stress release of beech mediated by admixture of different tree species (Pretzsch et al. 2012a, Condés et al. 2013, Río et al. 2014a, b, Cardil et al. 2018). Water availability is negatively correlated with iWUE (Waterhouse et al. 2004), so the decrease of iWUE as interspecific competition increases (González de Andrés et al. 2018) highlights a reduction of water stress, and thus a rise in stomatal conductance, in European beech trees growing in mixtures with Scots pine. We did not found significant growth responses of European beech to rising values of the interspecific competition index, what might be the result of social class of sampled beech trees (mainly dominant) and the highly efficient use of above- and belowground growing space of this species (Curt & Prevosto 2003, Dieler & Pretsch 2013) that could outcompete Scots pine. The water-related character of mixing effects on European beech is endorsed by simulations with FORECAST Climate because a reduction in canopy transpiration per tree is predicted for beech when Scots pine is admixed, especially under climate change scenarios (González de Andrés et al. 2017). Globally, our results suggest that European beech trees growing in mixtures with Scots pine would face more favourable conditions under warmer and drier climate than in pure stands. This agrees with other empirical (Cardil et al. 2018) and inventory-based studies (Río et al. 2014a) conducted in Pyrenean mixed forests of Scots pine and European beech.

The reported patterns in complementarity were consistent with the "complementarity – competition" framework (Forrester & Bauhus 2016), which states that complementarity between species increases along spatial and temporal gradients as long as mixing effects improve availability,

uptake or use efficiency of the resource that becomes more limiting. In the forest stands of this research water is proposed to exert the greatest limitation, especially at the Mediterranean site (Primicia et al. 2013, Cardil et al. 2018), so species interactions resulted in growth reductions for Scots pine and neutral or positive effects for European beech likely due to the contrasting character of the interactions of both species. Therefore, as other recent researches have highlighted (Grossiord et al. 2014b, Lübbe et al. 2015, Dziedek et al. 2016, Forrester et al. 2016, Metz et al. 2016, Vitali et al. 2018), both empirical and modelling results emphasize the importance of considering the species identity or functional traits involved in a given species combination when assessing their response to global change drivers.

Species characteristics and climatic and local conditions give rise to great variety of growth responses to water use, which have been reported to be positive (Martínez-Vilalta et al. 2008, Silva & Anand et al. 2013, Tegel et al. 2014), neutral or negative (Peñuelas et al. 2011, Silva & Anand et al. 2013, Granda et al. 2014, Lévesque et al. 2014). We have found that growth – iWUE relationships contrasted between both tree species. Increases in iWUE did not translate into growth enhancement for Scots pine at none of the sites (González de Andrés et al. 2018) likely as a consequence of a combination of water (Lévesque et al. 2014) and nutrient (Hobbie & Colpaert 2004) limitations. Meanwhile, growth – iWUE relationship was positive for European beech, particularly at the Mediterranean site, although this relationship does not present consistent results along the south-edge populations of this species as positive growth responses (Tegel et al. 2014) as well as negative have been reported (Piovesan et al. 2005, Peñuelas et al. 2008). In any case, our results reveal a progressive uncoupling among beech's growth, iWUE and rising atmospheric CO_2 concentration along the 20th century and a diminishing CO_2 fertilization effect on European beech in the same line than other results for this and other species (e.g. Waterhouse et al. 2004, Peñuelas et al. 2008, Linares et al. 2009, Linares & Camarero 2012). As a consequence of the absence (Scots pine) or drop (European beech) of the long-term CO_2 fertilization effect, the capacity of C sequestration of these widely distributed mixtures may be lower than projected.

Growth of trees is also determined in part by the nutrients reaching the soil, which are in turn defined by litterfall production, nutrient composition and stoichiometry (Kavvadias et al. 2001). The gathering of one of the longest litterfall series of mixed forests in Europe (16-year series) has facilitated the establishment of relationships among different forest processes and to better understand the dynamics of energy and nutrients transfer from trees to soil and vice versa (Chapter 3). Leaf fall seasonality and composition are important factors affecting nutrient cycling in forest ecosystems, and they differ among species (Prescott 2002). Therefore, the spread of European beech crown cover, whose leaf litter exhibits higher concentration of nutrients, may have hastened decomposition rates thus accelerating nutrient return to soils. In fact, faster nutrient cycles have been proposed as one of the causes promoting mixing effects in mixed-species forests (Forrester et al. 2005), which is supported by our FORECAST Climate simulations (González de Andrés et al. 2017). Testing this hypothesis in our experimental forests may constitute an interesting subject for future research.

We have found that seasonality and chemical composition of leaf litter of both species, the biggest fraction of litterfall, was strongly impacted by soil water availability (Chapter 3). This finding provides empirical evidence to the linkage between different resources limitations and highlights the important role of water availability because it not only has direct effect on meristems' activity but also on the nutrient supply of trees. Consistent with other studies of pine species in water-limited environments (Pausas 1997, Berg & Meentemeyer 2001, Martínez-Alonso et al. 2007), our results show that the drier the summer conditions, the earlier the Scots pine needle fall. Meanwhile, autumn storms may produce premature abscission of European beech leaves likely as a result of the physical impact of heavy precipitation events. Soil water content was positively associated with [N] and [P] and negatively with N:P ratios of leaf litter of both species (Chapter 3). Droughts have been found to impact nutrient availability (through nutrient mobility and mineralization), nutrient allocation to different tree organs (Sardans et al. 2012a, 2017), and resorption of nutrients during senescence (Del Arco et al. 1991, Yuan & Chen 2009). Although we cannot disentangle the relative contribution of each of those processes, we can state that altogether the impact of water availability on leaf litter composition differs between both nutrients, thus explaining the reported increases in N:P ratio as water supply becomes more limiting. In any case, Blanco et al. (2009) and Primicia et al. (2014) reported higher N:P ratios in green pine needles than the ratios we have found in senescent needles, which indicates that pine trees resorb more P than N during senescence. Conversely to [N] and [P], [K] in leaf litter was shown to increase with water shortage, particularly for European beech. K is involved in the tree water balance with important roles on stomatal function (Khosravifar et al. 2008), control of osmosis (Babita et al. 2010) and hydraulic conductance of water (Oddo et al. 2011), and has been found to be related with drought resistance in Mediterranean forests (Sardans et al. 2013) as it is allocated to leaves during water stress episodes (Sardans et al. 2012b).

The influence of climatic conditions on litterfall is usually evaluated measuring local climate variables. However, litterfall – local climate relationships may be complex and temporally variable, so the novel assessment of the connection between leaf litter dynamics and large-scale atmospheric-oceanic circulation patterns can provide an insight of changes in local physical environment and ecological processes (Stenseth et al. 2002). Indeed, large-scale climatic indices, such as NAO and ENSO through their influence on water availability in the Pyrenees, accounted for similar and even higher variability of leaf litter production and composition than local climate variables (Chapter 3). Large-scale circulation indices have outperformed proxies of local climate in plant phenology (Post & Stenseth 1999, Guan 2014) and tree growth studies (Camarero et al. 2011, Guan et al. 2012, Rozas et al. 2015, Lo et al. 2017, Guan et al. 2018, Madrigal-González et al. 2018). Considering the projected futures changes in NAO and ENSO (Christensen et al. 2013), a better understanding of the connection between nutrient return to forest soils through litterfall and large-scale circulation patterns could help to improve predictions of forest functioning in response to changes in climatic conditions. Incorporating such variables into forest models such as FORECAST Climate can be subject of future research, since the large-scale climatic indices are broadly accessible and could solve the problem of the lack of climate records for some regions.

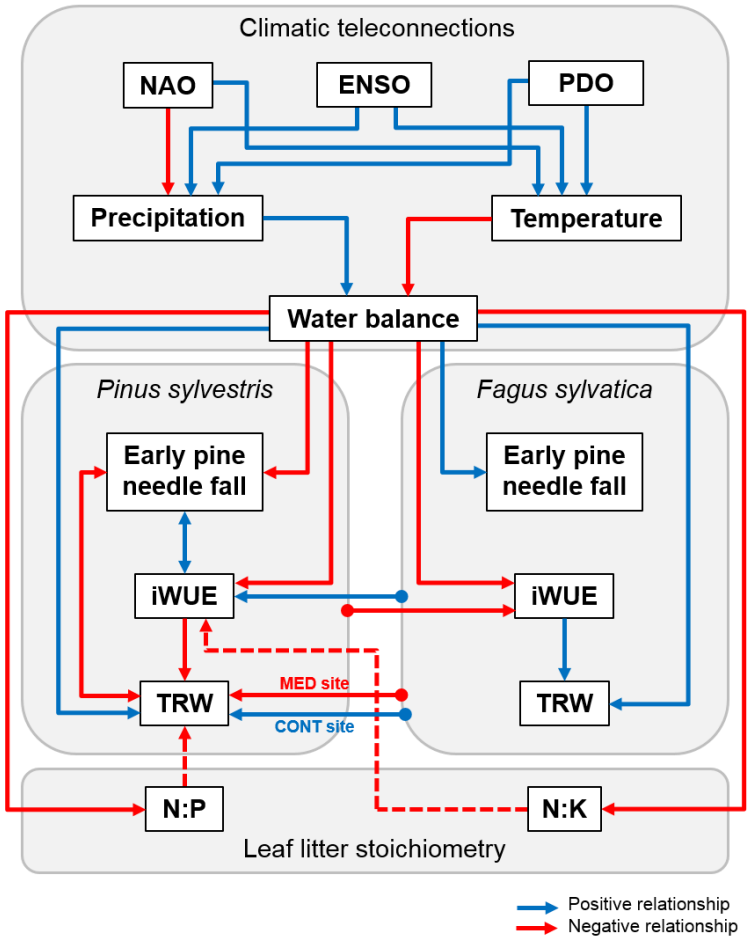

Figure 1. Conceptual model summarizing findings reported in this thesis research. Blue and red lines correspond with positive and negative relationships, respectively. Large-scale oscillatory patterns (North Atlantic Oscillation, NAO; El Niño – Southern Oscillation, ENSO; Pacific Decadal Oscillation, PDO) are related with local climatic conditions of the southwestern Pyrenees ('Climatic teleconnections'), which in turn are connected with the response of different ecosystem components. Tree level responses regarding timing of leaf abscission, intrinsic water-use efficiency (iWUE) and tree-ring width (TRW) are included in grey boxes corresponding to study species: Scots pine (*Pinus sylvestris*) and European beech (*Fagus sylvatica*). Arrows connecting different species represent interspecific interactions. Stoichiometric ratios (N:P and N:K) of the combination of leaf litter of both species are related to growth and iWUE of Scots pine; dash arrows represent an indirect relationship through decomposition and nutrient release processes with a time lag of 3 years between leaf fall and tree-ring formation.

N:P:K stoichiometry of litterfall has an essential role regulating forest functioning due to its impact on decomposition rates and nutrient release, and therefore their subsequent availability for other plants and soil organisms (Berg & McClaugherty 2003, Mooshammer et al. 2012). Therefore, litterfall stoichiometry can reflect constraints on internal fluxes of nutrients at the ecosystem scale (Vitousek 1982, McGroddy et al. 2004, Zechmeister-Boltenstern et al. 2015). The consumer-driven nutrient recycling theory predicts that the ratios of nutrient recycling in the ecosystem are influenced by the stoichiometric balance between litterfall and soil microbes (Sterner & Elser 2002). Following the N:P threshold proposed by Güsewell & Freeman (2005), leaf litter decomposition in the study pine-

beech mixtures could be limited by P particularly at the Mediterranean site (Chapter 3), thus reducing nutrient return to soil. This result agrees with the P immobilization during decomposition of pine needles reported by Blanco et al. (2011). Accordingly, P limitation has been suggested in these forests (Blanco et al. 2009, Primicia et al. 2014) and other Scots pine and European forests of Central Europe (e.g. Jonard et al. 2015, Talkner et al. 2015, Hofmann et al. 2016). Rising atmospheric N deposition has been identified as a main cause of P nutrition deterioration of natural and managed ecosystems (Peñuelas et al. 2013). Likewise, an increase in N deposition in the northern mountains of the Iberian Peninsula has been reported (Ávila & Rodá 2012), so identifying a high risk of N saturation (García-Gómez et al. 2014, Blanco et al. 2017). Site-specific factors (i.e. fertilization practices in surrounding lands) may also contribute to close N saturation situations.

Finally, we have found a negative relationship between Scots pine tree growth and N:P ratios of leaf litter (considering the proportional contribution of both pine and beech) fallen three years prior tree-ring formation (Chapter 3). We interpreted this result in the light of the growth rate hypothesis (Sterner & Elser 2002) as low litter N:P ratios are required to maintain the elevated growth rate of soil microbes. Besides, we have found a close association between leaf litter N:K ratio and pine iWUE, again with a 3-year time lag, which highlights the important role of K in the regulation of tree water balance (Chapter 3). Indeed, field-based evidence of growth and water use associations with leaf litter stoichiometry may support the explanation of nutrient-mediated uncoupling of growth – iWUE in Scots pine trees (González de Andrés et al. 2018). The simultaneous connections between forest processes and resources limitations reported along this thesis research (i.e. N:P – growth, N:P – water availability, N:K – iWUE, growth – water availability, growth – iWUE), which are outlined in a conceptual framework in the Figure 1, underscore the intricate relationships among water and nutrient supplies and forest functioning. Therefore, a clearer establishment of these relationships at empirical level could grant revisiting FORECAST Climate simulations (González de Andrés et al. 2017) as a lack of understanding of the factors influencing stoichiometry limits their incorporation into ecological models (Yuan & Chen 2015).

Improving the knowledge of Scots pine and European beech mixed forest functioning may help to understand the behaviour of other mixed-species forests composed by different species with comparable functions, that is coniferous-broadleaf mixtures from temperate and Mediterranean regions. That would be the case of the widespread Norway spruce (*Picea abies* [L.] Karst.) and European beech mixed forests, which are the most investigated mixtures in central Europe. Indeed, scientific research focused on each of the two species combinations has fed each other. Transgressive overyielding (i.e. the growth of the mixed stand exceeds the growth of the pure stand of the best growing species in the mixture) has been reported in spruce-beech mixtures (Pretzsch & Schütze 2009) due to spruce facilitation by nutrient pumping of deeper rooting beech (Bolte & Villanueva 2006) and the reduction of self shading of beech trees (Dieler & Pretzsch 2013). Although differences might be expected between Norway spruce and Scots pine owing to morphological and physiological dissimilarities, both coniferous species may play analogous roles when admixed to European beech (Metz et al. 2016). Furthermore, Scots pine may also grow in mixtures with Mediterranean oaks at its southern edge of distribution. For instance, Río & Sterba (2009) reported complementearity between Scots pine and Pyrenean oak (*Quercus pyrenaica* Willd.) growing together in central Spain.

Mediterranean oaks are less productive and more resistant to drought than European beech, however the deep rooting system and deciduous character are common traits for both broadleaves that can make their mixtures with Scots pine comparable systems.

A decrease in nutrient uptake and deterioration of nutritional status of Pyrenean mixed forests of Scots pine and European beech could happen under the predicted increase in atmospheric N deposition and the intensification of dry spells for this region, considering the close association between water availability, leaf litter dynamics and nutrient return to soils. Consequently, negative direct impacts of droughts on tree growth may be worsened by reducing capacity of trees to use water efficiently. Besides, the interaction with other global change drivers, such as rising atmospheric CO_2 concentration or biotic invasions, and the historical land uses could introduce further complexity, because their effects can be synergistic or antagonistic, not simply additive (Sardans et al. 2017). In fact, Lo et al. (2015) estimated from a modelling approach significant reductions in C and N stocks of the two study forests as a consequence of changes in land uses from forested areas to pastures and crops and back to secondary forests during the last two centuries.

Globally, this thesis research suggests a potential benefit for European beech growing in mixtures with Scots pine, whereas Scots pine could be harmed unless the increasing co-limitation by water and nutrients is counteracted by beech facilitation. Therefore, in order to assure forest productivity and resilience of mixed-species forests in general, and Scots pine – European beech mixtures in particular, management plans need to consider the simultaneous effects of historical land uses and different resource limitations predicted under global change scenarios, and their impact on intra- and interspecific tree-to-tree interactions.

Practical management recommendations can be outlined. Considering the differing effects of intra- and inter-specific competition on both Scots pine and European beech functioning, spatial distribution of tree species at small spatial scales (up to 9 m for Scots pine and 5 m for European beech, González de Andrés et al. 2018) need to be regarded when designing mixed-species plantations or conversions from pure forests to mixtures. In the view of our results, mixing configurations with close inter-specific intermingling could improve performance of both species as it promotes the reduction of self-competition and enhace the potential benefits of inter-specific interactions (González de Andrés et al. 2017, 2018). Such recommendation is supported by findings reported for Norway spruce (*Picea abies* (L.) Karst.) and European beech mixtures in empirical (Pretzsch et al. 2012b) and modelling studies (Rötzer 2013). Stand density is also a key issue in mixed forests management since at low densities interactions may not be strong enough to impact trees functioning, while at high densities competition can outweigh complementarity effects (Condés et al. 2013, Forrester 2017). Indeed, thinning has been proposed as a strategy for mitigating drought stress for both Scots pine and European beech (Giuggiola et al. 2013, van der Maaten 2013, Sohn et al. 2016). At the drought-prone Mediterranean study site, Primicia et al. (2013) found that the negative effect of European beech on Scots pine growth could be relieved by thinning treatments, and Cardil et al. (2018) reported mitigation of growth reduction of both pine and beech during drought periods in thinned plots. Optimum tree spacing could be assessed in planted experiments, such as replacement series with different densities (Vanclay 2006, Bauhus et al. 2017), or in simulations at varying densities with

forest growth models (Candel-Pérez et al. 2017). Finally, the sustainability of silvicultural practices in heterogeneous regions such as the study area is strongly site dependent. However, the maintenance of adequate cycles of nutients such as N and P, which are essential for soil fertility and forest functioning, requires avoiding whole-tree harvesting (Blanco et al. 2005, Achat et al. 2015).

To summarize, the main general conclusions drawn from this study are:

- Scots pine trees can benefit from the admixture of European beech due to the complementary canopy structures of both species and synergistic effects regarding vertical structure heterogeneity, which may be boosted by improved nutrient supply as a result of beech leaf litter addition. However, the light-related mixing effects can be overridden by strong competition for water resources with European beech in drought-prone sites and under the prediction of drier conditions by climate change scenarios.

- The low self-tolerance of European beech may be partly alleviated as less water stress for this species has been found in mixtures with Scots pine compared with pure stands. Water-related mixing effects could provide advantage to beech trees growing in mixtures in the face of the expected increase of water shortage.

- Our results are consistent with the "complementarity – competition" framework, of which the stress gradient hypothesis is considered an special case, as complementarity decreased for Scots pine and increased for European beech along the gradient of the most limiting factor for these populations at the southern limit of species distribution , i.e., water availability.

- Leaf litter dynamics reflect the progressive natural succession towards mixed Scots pine and European beech forests during the last 16 years at the study sites, thus modifying nutrient return through litterfall to soils. However, N:P ratios of leaf litter show increasing trends. The consequent rise in P limitation might worsen the direct effects of drought on tree growth as indirect effect of water availability on nutrient inputs can reduce capacity of trees to use water efficiently.

- Large-scale circulation patterns, through their influence on water availability in the Pyrenees, account for some variability of leaf litter seasonality, nutrient composition and N:P:K stoichiometry of Scots pine – European beech mixtures. At the same time such leaf litter stoichiometry are connected with secondary growth and water-use efficiency of Scots pine. Together these findings provide an empirical evidence of the interconnection of water and nutrient limitation.

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APPENDIX A (Chapter 1)

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Table S1. Parameter estimates for the selected linear mixed-effects models fitted to explain changes in basal area increment (BAI) and intrinsic water use-efficiency (iWUE) of beech (*Fagus sylvatica*) at the Mediterranean site for the inner most tree-rings of trees belonging to two age groups: "old" (trees born before 1950) and "young" (trees born in or after 1950). Bold values indicate effects significant at $P < 0.05$. Only those factors of the best model obtained by minimizing the Akaike information criterion (AIC) are shown.

	R^2m	R^2c	Fixed effects	
BAI	0.860	0.860	C_a	**1.775**
			iWUE	**0.320**
			age group	**-1.895**
			C_a x age group	**-1.383**
iWUE	0.360	0.527	$P\text{-}PET_{sum}$	**-0.184**
			C_a	**1.272**
			age group	-0.391
			C_a x age group	**-1.269**

Fixed effects were: seasonal temperature (T) and water balance (P-PET), site, atmospheric CO_2 concentration (C_a), derived variable from the cambial age of the tree-ring (ageRes) and iWUE (only in the growth model). In the case of climate variables, subscripts correspond to seasons and "-1" indicates the year prior to tree-ring formation.

R^2m and R^2c correspond to marginal (proportion of variance explained by the fixed factors) and conditional (proportion of variance explained by fixed plus random factors) R^2 values, respectively, calculated following Nakagawa and Schielzeth (2013). Random factors were the trees nested in plots sampled at each site, being the residual variance $\sigma^2 = 0.328$ and $\sigma^2 = 0.634$ for BAI and iWUE models, respectively. A first-order autocorrelation structure was included in the models. An exponential variance structure associated with cambial age was also included in the growth model.

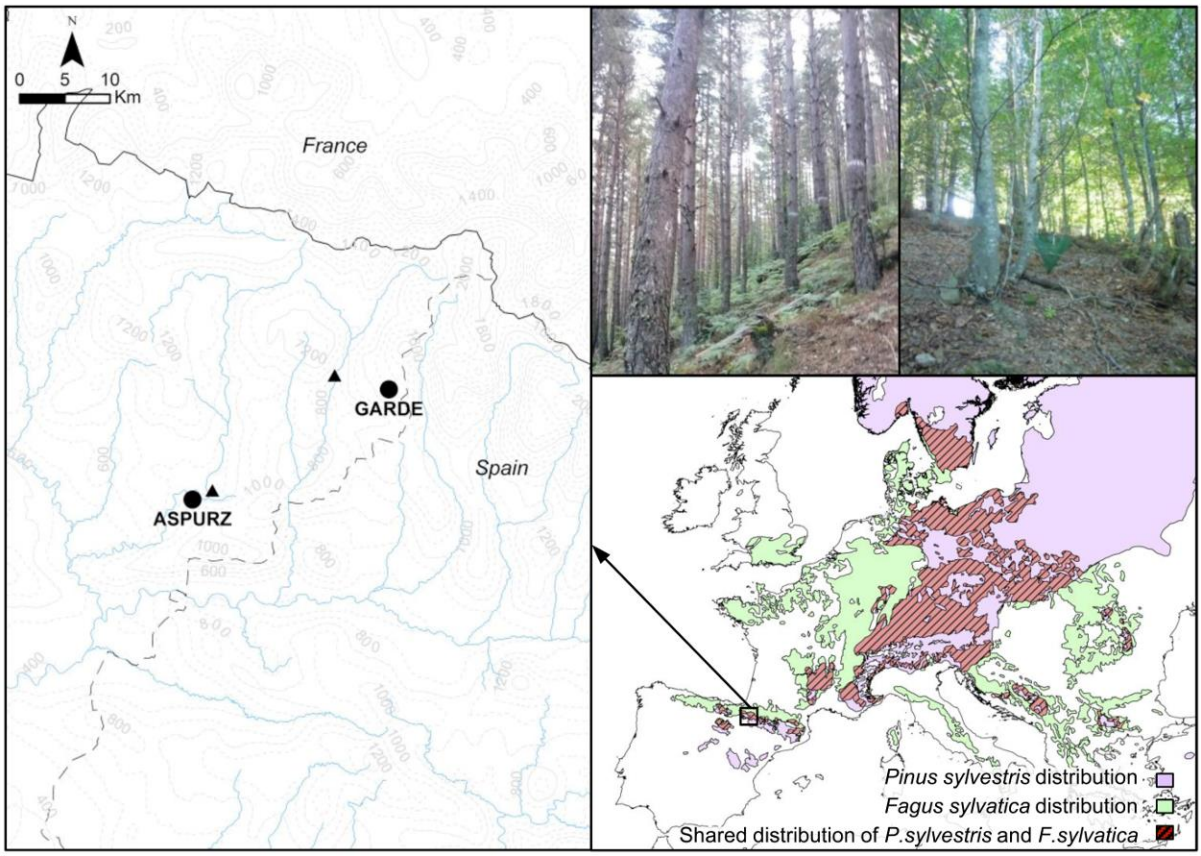

Figure S1. Location of experimental plots (circles) and weather stations providing climatic date (triangles). The map in the lower right shows the natural European distribution of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) (modified from EUFORGEN, 2009a, b) and the common area between both species. Upper right pictures show images from experimental pine (left) and beech (right) stands.

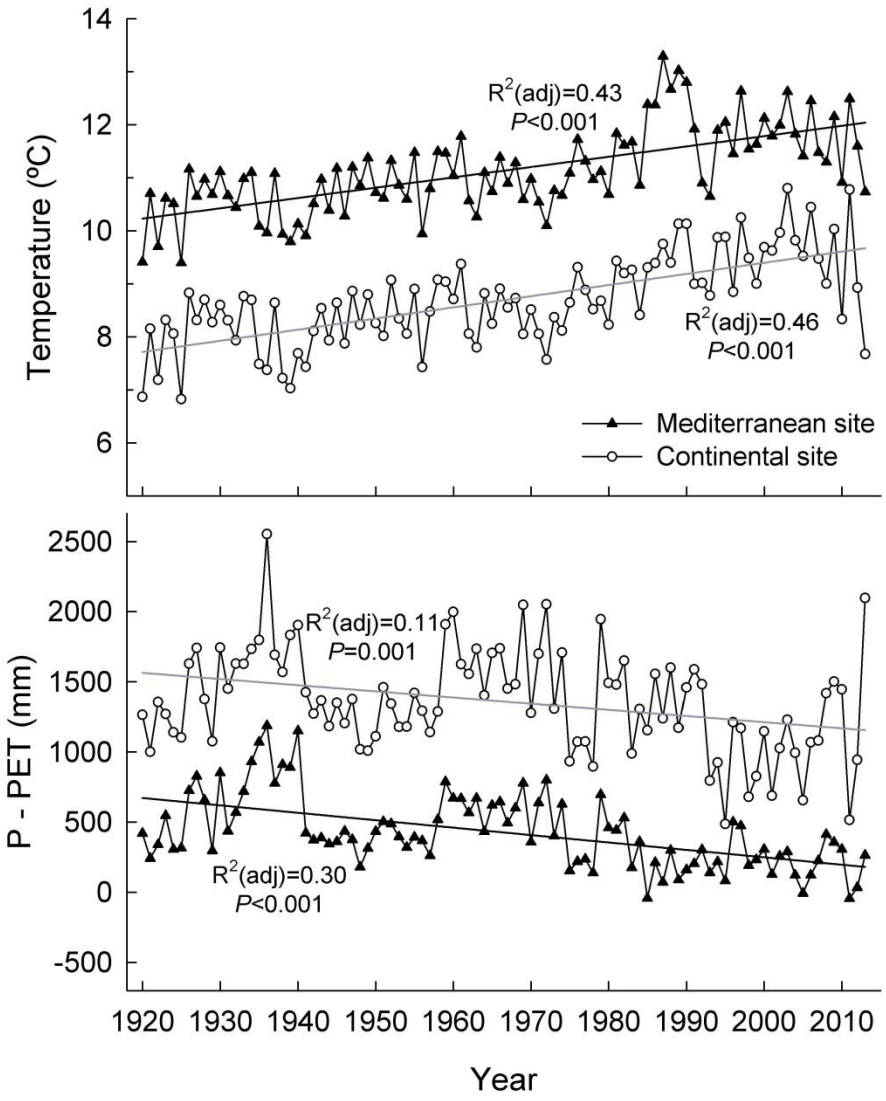

Figure S2. (A) Variation of mean annual temperature and (B) annual water balance, calculated as the difference between total precipitation (P) and potential evapotranspiration (PET), for the period 1920-2013 in the two study sites. Equations of simple linear regression showing climate trends are presented in the bottom of graphs.

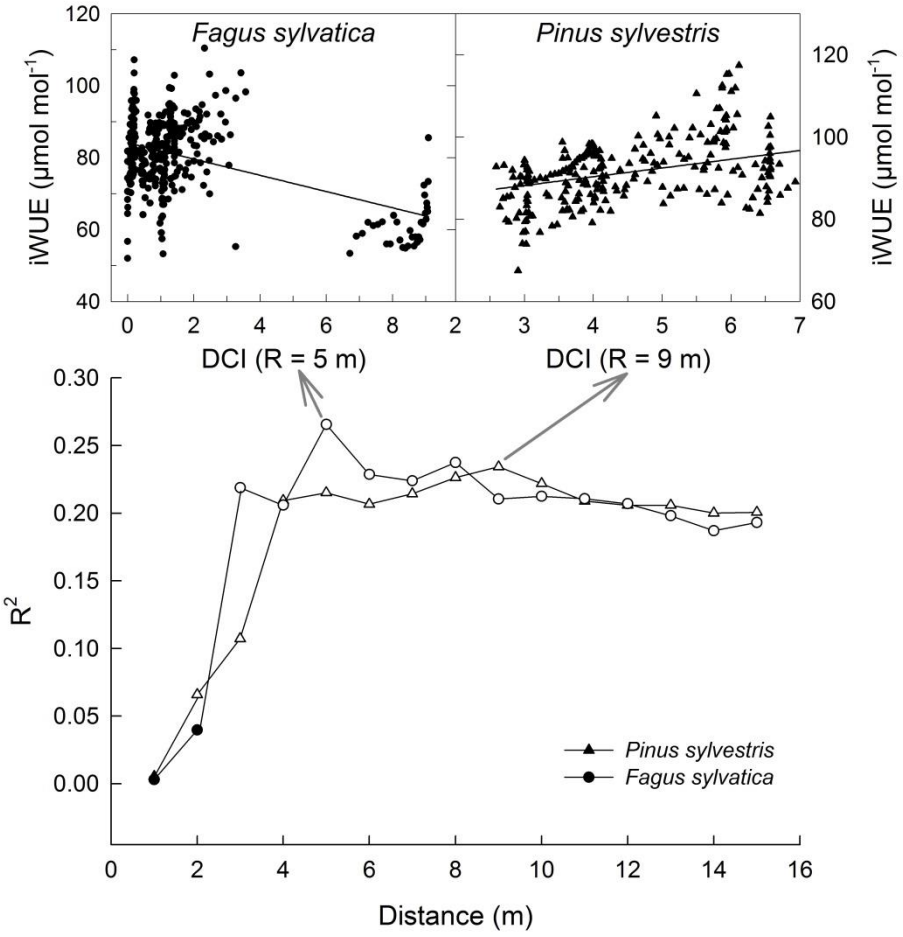

Figure S3. Coefficients of determination (R^2) obtained by relating the intrinsic water use-efficiency (iWUE) and the distance-dependent competition index (*DCI*) calculated by increasing the radii of the competition neighbourhood around the focal tree at 1-m intervals and from 1 to 15 m. *DCI* values are calculated considering both intra- and inter-specific competition. Significant values at the 0.05 level are indicated by empty symbols. The upper scatter plots represent the relationships between iWUE and *DCI* for the distance where the maximum correlation was found for Scots pine (top left) and for beech (top right).

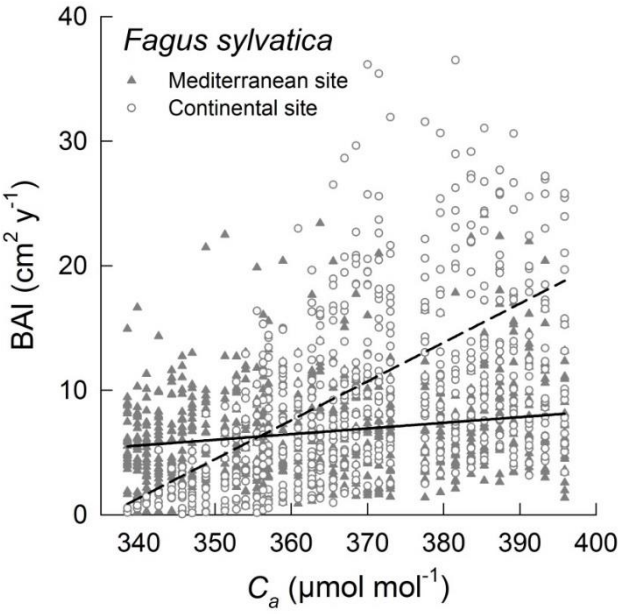

Figure S4. Relationship between basal area increment (BAI) and atmospheric CO_2 concentration (C_a) at the two study sites for European beech (*Fagus sylvatica*). The solid line represents the trend at the Mediterranean site and the dash line represents the trend at the continental site.

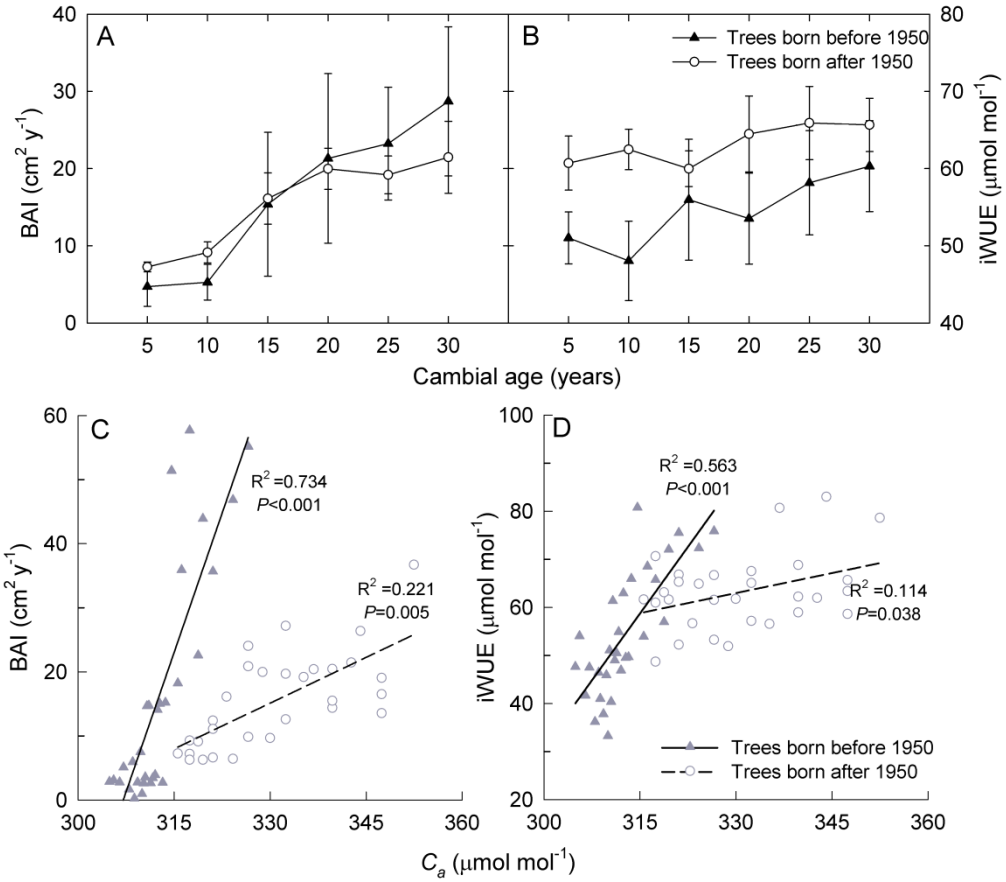

Figure S5. Variations in intrinsic water-use efficiency (iWUE; A) and basal area increment (BAI; B) of European beech trees (*Fagus sylvatica*) born before 1950 and after or in 1950 at the Mediterranean site. Data are aligned according to cambial age. Relationships observed between BAI and atmospheric CO_2 concentration (C_a; **C**), and between iWUE and C_a (**D**) for two age groups of beech.

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EUFORGEN (2009a) *Distribution map of Beech (Fagus sylvatica)*. http://www.euforgen.org.

EUFORGEN (2009b) *Distribution map of Scots pine (Pinus sylvestris)*, http://www.euforgen.org.

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142. https://dx.doi.org/10.1111/j.2041-210x.2012.00261.

APPENDIX B (Chapter 2)

1. MODELLING APPROACH

1.1. FORECAST-Climate development

FORECAST-Climate was developed from FORECAST (Kimmins et al. 1999) which is a managed-oriented, deterministic, non-spatial, stand-level forest growth and ecosystem dynamics simulator. FORECAST was designed to accommodate a wide variety of harvesting and silvicultural systems in order to compare and contrast their effect upon forest productivity, stand dynamics and a series of biophysical indicators of non- timber stand values. The model has been used in a wide variety of applications and has been evaluated against field data for growth, yield, ecophysiological and soil variables (e.g. Bi et al. 2007, Blanco et al. 2007, Seely et al. 2008). The model uses a hybrid approach to vegetation growth modelling, as it merges the use of empirical data modified by the simulation of the most important ecological processes (Kimmins et al. 1999, Landsberg 2003). Projection of stand growth and ecosystem dynamics is based on a representation of the rates of key ecological processes regulating the availability of, and competition for, light and nutrient resources (Fig. S1A). FORECAST assumes that climate for the simulated scenario is similar to the climate during the time when empirical data were recorded. However, the rising trends in greenhouse gas emissions and their associated impacts on future temperature and precipitation patterns (IPCC 2013) triggered the development of an explicit representation of moisture and temperature on ecosystem processes.

Hydrological processes are simulated by the forest hydrology model ForWaDy in which water flows through a layered forest ecosystem approach (Fig. S1B). General data requirements of ForWady are shown in Table S1. FORECAST and ForWaDy are dynamically linked to create FORECAST-Climate, as the respective functions from each model are continuously updated in response to the iterative sharing of information encoded within a series of feedback loops.

1.2. Climate impacts on productivity, decomposition and mortality

The impact of climate (temperature and moisture) on plant growth and decomposition processes is represented with species-specific curvilinear response functions simulated on a daily time step (Fig. S2). A net daily growth response index of species *i* and day *d* ($GRI_{Day\ i,d}$) and a daily decomposition response index of soil layer *l* and day *d* ($DRI_{Day\ l,d}$) are derived as the product of temperature and water stress components. Daily response indexes are then summed to calculate annual response indexes for growth ($GRI_{Year\ i,y}$) and decomposition ($DRI_{Year\ l,y}$). A calibration run is conducted with the reference climate data set from which t $GRI_{Year\ i,y}$ and $DRI_{Year\ l,y}$ are calculated. By averaging the annual values for the length of the reference climate period, a normalized growth and decomposition response indexes are derived for each species or soil layer that reflects 'normal' conditions in an average historical climate year. Annual climate response indexes are compared against normalized response indexes to obtain climate factors, which modify base growth and decomposition rates to achieve a climate-limited growth and decomposition (Eq.S1 & S2).

$$CRF_{i,y} = (GRI_{Year\ i,y} - NGRI_i) / NGRI_i \text{ and } CDF_{x,y} = (DRI_{Year\ l,y} - NDRI_l) / NDRI_l \quad \text{(Eq. S1)}$$

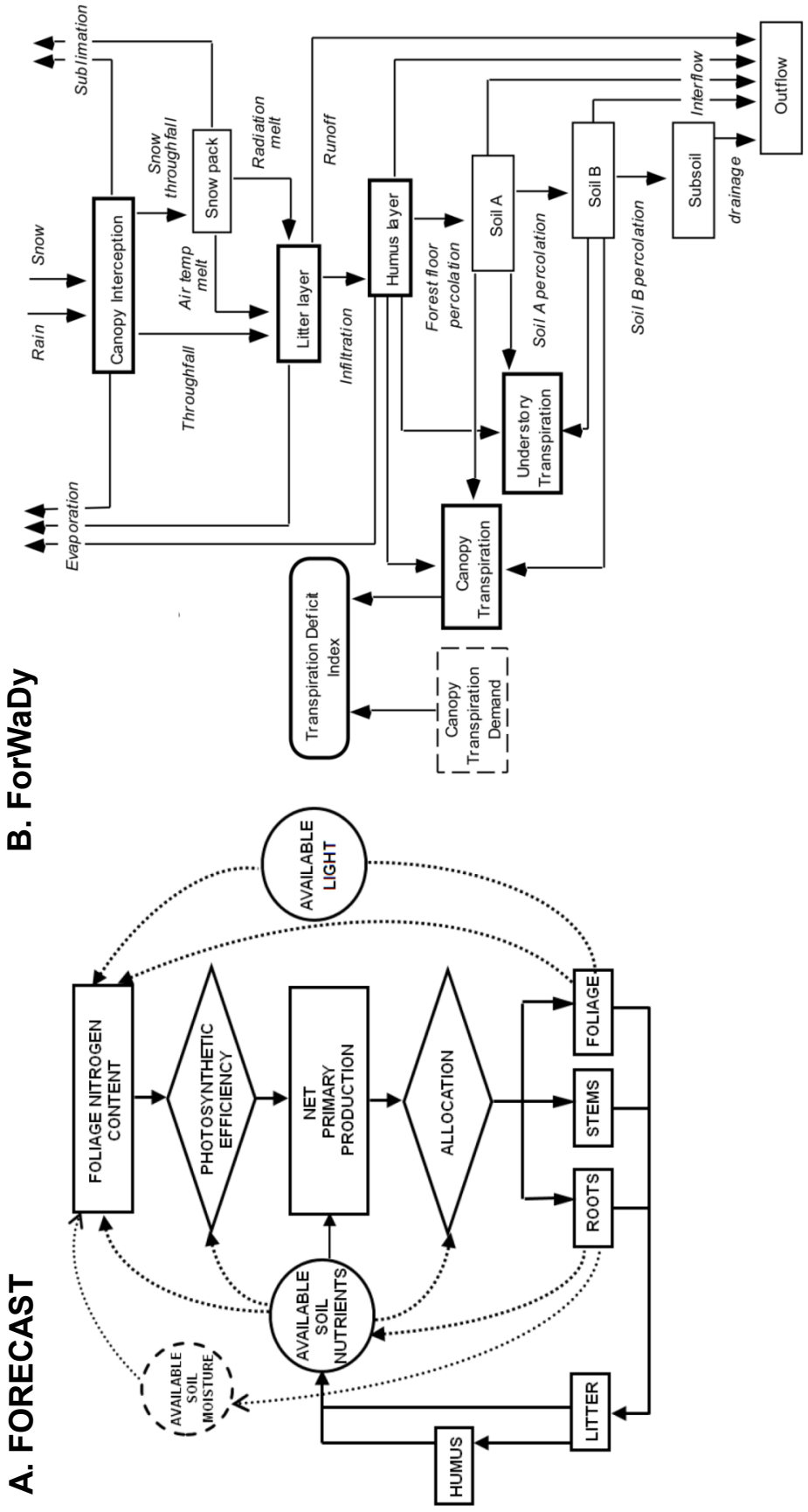

Figure S1. Schematic representation of: (A) key ecosystem processes and interactions (black dotted lines), and mass flows between ecosystem pools (black solid lines) represented in FORECAST model (after Blanco 2012); and (B) the forest hydrology model ForWaDy indicating water flow pathways and storage compartments in the model (after Seely et al. 1997), used to estimate the available soil moisture in FORECAST.

$$CGR_{i,y} = BRG_{i,y} * CRF_{i,y} \text{ and } CDR_{x,y} = BRD_{x,y} * CDF_{x,y} \quad \text{(Eq. S2)}$$

where, $CRF_{i,y}$ is the climate response factor for species *i* in year *y*; $CDF_{x,y}$ is the climate decomposition factor for litter type *x* in year *y*; $NGRI_i$ and $NDRI_l$ are normalized growth and decomposition rates, respectively, derived from the reference climate; $CGR_{i,y}$ is the climate-limited growth rate for species *i* in year *y* (Mg ha^{-1}); $CDR_{x,y}$ is the expected climate decomposition rate for litter type *x* and year *y* (Mg ha^{-1}); $BRG_{i,y}$ is base growth rate determined in FORECAST as the light and nutrient-limited growth rate ; and $BRD_{x,y}$ is the base decomposition rate for each litter type determined as a function of litter quality.

Drought mortality is also included in FORECAST-Climate since long dry periods can cause plant individual loss, either directly or by increasing vulnerability to biotic disturbance agents (Allen et al., 2010). Water stress mortality is simulated through a user-defined graphical function of species-specific, two-year running average TDI (Fig. S3). For further details on impacts of increasing CO_2 on forest growth, linkage between FORECAST and ForWaDy and climate response factors of growth and soil related processes calculation see Seely et al. (2015).

Table S1. General data requirements for the ForWaDy model.

Climate data (daily)	Vegetation data	Forest floor and soil data
Mean, max and min air temperature (ºC)	Seasonal tree Leaf Area Index (LAI)	Fine litter mass (kg.ha^{-1})
Solar radiation (MJ. m^2).	Seasonal understory cover (%).	Humus layer depth (cm) and bulk density (g.cm^3)
Total precipitation (mm).	Rooting depth for trees (cm)	Depth of mineral soil layers (rooting depth) (cm)
Snow fraction.	Rooting depth for understory (cm)	Soil texture class of each soil layer
Atmospheric [CO_2].	Canopy resistance and albedo (by species)	Coarse fragment content (> 2 mm) in each soil layer

1.3. Model validation and sensitivity analysis

FORECAST and FORECAST Climate models have been successfully validated for a wide range of forests types including six different biomes during the last 30 years (Table S2). The model has not been fully evaluated for Scots pine-European beech mixtures of the Pyrenees, so the predicted values may be not exact. However, the fact that the model is able to adequately simulate main forest processes in a wide range of situations allow us to be confident when comparing different pure-mixed conditions and climatic scenarios. Therefore, we are confident that trends and relative differences among scenarios (if not the exact values) are adequately represented. In addition, several sensitivity analyses have been conducted (Table S3). They pointed out that the model is sensitive to key parameters of mixed-species forests, such as species proportion or root biomass and decomposition but also robust against extreme parameter values, and therefore we are confident that the model adequately represents growth trends for the expected value ranges of the key parameters.

Table S2. List of validation studies for different versions of FORECAST growth model.

Biome	Forest type	Species	Country	Variables	Reference
Boreal	Coniferous	*Picea glauca*	USA (Alaska)	Stand density, nitrogen fluxes	Yarie 1986
Boreal	Mixed conifer-broadleaf	*Pinus contorta var. latifolia, Picea glauca, Populus tremuloides*	Canada (B.C.)	Carbon pools	Seely et al. 2002
Sub-boreal	Mixed conifer-broadleaf	*Picea glauca*, *Populus tremuloides*, *Pseudotsuga menziesii*, *Betula papyrifera*	Canada (B.C.)	Biomass, tree height, diameter	Seely et al. 2008
Temperate	Coniferous	*Pseudotsuga menziesii*	Canada (B.C.)	Stand density, tree height, diameter	Sachs & Trofymow 1991
Temperate	Coniferous	*Pseudotsuga menziesii*	Canada (B.C.)	Biomass pools	Blanco 2007
Temperate	Coniferous	*Pseudotsuga menziesii*	Canada (B.C.)	Biomass pools, stand density, tree height, diameter	Blanco et al. 2007
Temperate	Coniferous	*Pseudotsuga menziesii*	Canada (B.C.)	Biomass pools, stand density, tree height, diameter	Kimmins et al. 2008
Temperate	Coniferous	*Picea asperate*	China (W)	Biomass pools	Jie et al. 2011
Temperate	Broadleaf	*Populus tremuloides*	USA (Wisconsin)	Carbon and nitrogen pools	Wang et al. 2014
Mediterranean	Coniferous	*Pinus sylvestris*	Spain (Navarra)	Biomass pools	Blanco et al. 2006c
Mediterranean	Coniferous	*Pinus sylvestris*	Spain (Navarra)	Carbon and nitrogen pools	Lo et al. 2015
Subtropical	Coniferous	*Cunninghamia lanceolata*	China (Zhejiang)	Biomass pools, soil organic matter	Bi et al. 2007
Subtropical	Coniferous	*Cunninghamia lanceolata*	China	Stand density, tree height, diameter	Ding & Tian 2009
Subtropical	Coniferous	*Cunninghamia lanceolata*	China (SE)	Biomass, tree height, diameter	Blanco et al. 2012a
Subtropical	Coniferous	*Metasequoia glyptostroboides*	China (Shanghai)	Biomass, tree height, diameter	Zheng et al. 2018
Subtropical	Coniferous	*Cunninghamia lanceolata*	China (Fuijan)	Weekly productivity	Kang et al. 2017
Subtropical	Mixed conifer	*Toona ciliata*, *Pinus taeda*, *Pinus elliotti*	Argentina	Soil water, mortality	Dordel et al. 2011
Subtropical	Broadleaf	*Phoebe bourneii*	China (SE)	Biomass pools, stand density, tree height, diameter	Wang et al. 2013
Subtropical	Mixed conifer-broadleaf	*Cunninghamia lanceolata*, *Phoebe bourneii*	China (SE)	Carbon pools	Wei & Blanco 2014
Tropical	Coniferous	*Pinus caribaea*	Cuba	Biomass, tree height, diameter	Blanco & González 2010a

Table S3. List of sensitivity analyses performed with FORECAST and FORECAST Climate growth model.

Biome	Forest type	Species	Country	Variables	Reference
Tropical	Coniferous	*Pinus caribaea*	Cuba	Carbon and nitrogen pools	Blanco & González 2010b
Temperate	Coniferous	*Pseudotsuga menziesii*, *Pinus contorta*, *Picea glauca*	Canada (B.C.)	Decomposition rates, soil organic matter pools	Seely et al. 2010
Temperate	Coniferous	*Pseudotsuga menziesii*	Canada (B.C.)	Carbon and nitrogen pools	Blanco 2012
Subtropical	Coniferous	*Cunninghamia lanceolata*	China (SE)	Deposition rates and root occupancy	Blanco et al. 2012b
Mediterranean	Coniferous	*Pinus sylvestris*	Spain (Navarra)	Root biomass, root decomposition rates, root nitrogen	Gárate & Blanco 2013
Sub-boreal and temperate	Mixed conifer-broadleaf	*Pinus contorta*, *Populus tremuloides*, *Picea mariana*, *Pseudotsuga menziesii*	Canada (B.C.)	Decomposition rates, soil organic matter pools	Blanco et al. 2015
Tropical	Mixed broadleaves	*Cinnamomum camphora*, *Fraxinus griffithii*	Taiwan	Stand density, mixing ratios	Wu et al. 2015
Mediterranean	Mixed conifer-broadleaf	*Pinus sylvestris*, *Fagus sylvatica*	Spain (Navarra)	Stand density, mixing ratios	Cándel-Pérez et al. 2017
Temperate	Mixed conifer-broadleaf	*Pinus contorta, Populus tremuloides*	Canada (B.C.)	Coarse woody debris, root decomposition rates	Blanco et al. 2018

1.4. Model calibration and initialization

Published yield tables and biomass equations were used to build historical *P. sylvestris* (García & Tella 1986, Puertas 2003) and *F. sylvatica* (Madrigal et al. 1992, Santa Regina & Tarazona 2001, Traver et al. 2007) growth patterns (age-biomass curves). Data on tree light and nitrogen requirements were derived from field data (Blanco et al. 2009, Primicia et al. 2014) and literature (Oliver & Larson 1996, Terradas 2001, Santa Regina & Tarazona 2001, Dufrene et al. 2005, Balandier et al. 2010). Literature data were also used to calibrate shading (Pretzsch et al. 2015) and turnover rates (Mäkelä & Vanninen 2000, Mainiero & Kazda 2006, Finér et al. 2007). Litter production was derived from field data (Kimmins 2004, Blanco et al. 2006a). Decomposition rates and soil data were derived from field data (Blanco et al. 2011, Fernández 2013, Martínez 2015) and literature (Blanco et al. 2006b). Empirical data showed the absence of N fixation in *P. sylvestris* stands (Blanco et al. 2016), therefore non-symbiotic N fixation was restricted to *F. sylvatica* wood and foliage litter. Atmospheric deposition rates are based on García-Gómez et al. (2014) predictions, and mineral weathering rates are from literature (Kimmins 2004, Fisher & Binkley 2000). Understory growth patterns (limited in the simulation to *Rubus* spp., the main dominant understory species by biomass at both sites; Arias 2014), nutrient concentration and litterfall decomposition rates were derived from literature (Mitchell et al. 2000, Imbert et al. 2008, García Del Barrio 2000) and field data (Arias 2014). Values of soil and tree-related parameters can be found in Table S4 and Table S5, respectively.

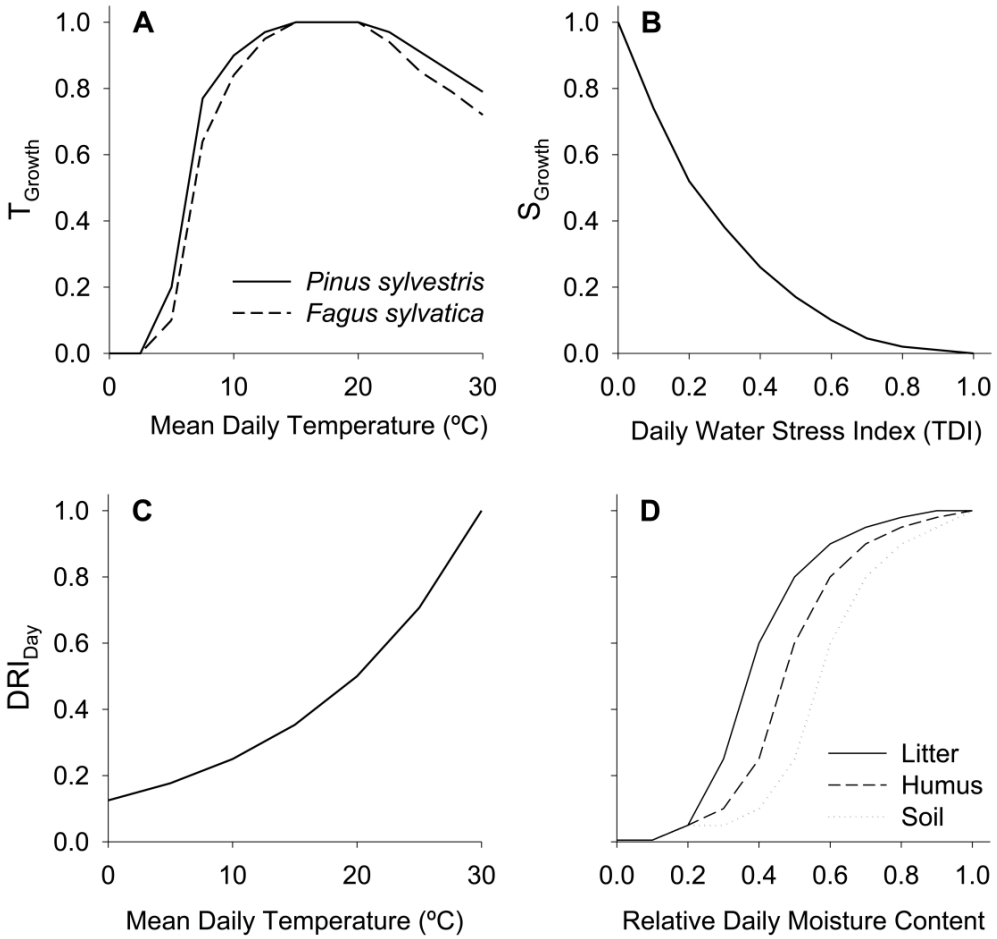

Figure S2. Climate response function showing the effect of temperature and water stress on growth (A, B) and decomposition (C, D). Relationships between mean daily temperature and a temperature growth modifier for both tree species (A), and daily water stress and moisture growth modifier (B). Daily decomposition index in relation to daily air temperature (C), based upon a Q_{10} function where $Q_{10} = 2$, and relative daily moisture content shown for litter, humus and mineral soil (D).

Seasonal changes in leaf area index (LAI) needed for ForWaDy model calibration were estimated with data from PEP725 Pan European Phenology Data (http://www.zamg.ac.at/ pep725/) and literature (Gill et al. 1998, Vitasse et al. 2009), whereas seasonal understory cover was derived from field data. Literature data were used for rooting depth of trees and understory vegetation (Fotelli et al. 2001, Bonnemann 1939 in Pretzsch et al. 2015), and canopy resistance and albedo (Otto et al. 2014). The climate response functions within FORECAST Climate were calibrated using historical daily climate data (see section 2.1.). Solar radiation was estimated from maximum and minimum air temperature, elevation, latitude, slope and aspect of study sites using published radiation models (Seely et al. 2015).

To establish initial site conditions we carried-out a modified version of the typical spin-up process used to let the model reach a stable state (Hashimoto et al. 2011, Shi et al. 2013). Initial conditions were created by running the model for ten 150-year cycles ending with a clear-cutting and

harvest of 90% of logs and allowed for a new cohort of trees to grow (Blanco et al. 2007, Blanco & González 2010a). Simulated stands were pine-beech mixtures. These runs allowed the model to accumulate soil organic matter (SOM) until reaching a stable value (378.1 and 506.3 Mg ha^{-1} for the high and low elevations sites, respectively). The final products of these runs were used as the starting conditions for the simulations.

Table S4. Values used to calibrate FORECAST parameters related to soil and geochemical cycles.

Parameter	**Mediterranean site** (Aspurz)	**Continental site** (Garde)
N concentration in slow / fast humus (%)	2.50 / 1.20	2.50 / 1.20
Decomposition rate slow / fast humus (% $year^{-1}$)	0.25 / 1.30	0.25 / 1.20
CEC soil (CEC humus) / AEC [a] (kg $N.ha^{-1}.year^{-1}$)	85.0 (0.1) / 2.0	50.0 (0.1) / 1.0
Atmospheric deposition / seepage (kg $N.ha^{-1}.year^{-1}$)	10.5 / 0.35	6.5 / 0.0
Initial SOM [b] (humus + litter) (Mg $.year^{-1}$)	506.27	378.08

[a] CEC: cation exchange capacity; AEC: anion exchange capacity
[b] SOM: soil organic matter

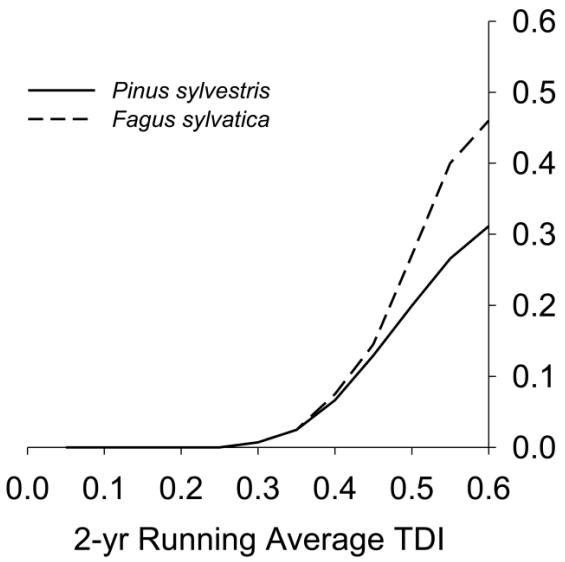

Figure S3. The drought-related mortality rate as a function of the 2-year running average water stress index.

Table S5. Values used to calibrate FORECAST parameters related to *Pinus sylvestris* and *Fagus sylvatica*.

	Pinus sylvestris		***Fagus sylvatica***	
	Mediterranean site (Aspurz)	**Continental site** (Garde)	**Mediterranean site** (Aspurz)	**Continental site** (Garde)
Nitrogen concentration in leaves young/old/dead (%)	1.40/1.35/0.64	1.10/1.06/0.68	1.53/1.53/0.72	1.26/1.26/0.66
Nitrogen concentration in stem sapwood/heartwood (%)	0.11 / 0.09	0.10 / 0.04	0.32 / 0.27	0.30 / 0.26
Nitrogen concentration in bark live/dead (%)	0.38 / 0.33	0.25 / 0.19	0.45 / 0.45	0.38 / 0.38
Nitrogen concentration in branches live/dead (%)	0.53 / 0.31	0.36 / 0.11	0.65 / 0.64	0.58 / 0.55
Nitrogen concentration in root sapwood/heartwood (%)	0.53 / 0.31	0.25 / 0.23	0.65 / 0.64	0.57 / 0.53
Nitrogen concentration in fine roots live/dead (%)	0.96 / 0.62	0.86 / 0.57	1.00 / 0.90	0.85 / 0.75
Shading by maximum foliage biomass (% of full light)	0.15	0.25	0.02	0.08
Soil volume occupied at maximum fine root biomass (%)	0.97	0.97	0.97	1
Efficiency of N root capture (%)	1	1	1	1
Retention time for young/old foliage/dead branches (years)	1 / 3 / 10	1 / 4 / 22	1 / 0 / 10	1 / 0 / 20
Fine roots turnover ($years^{-1}$)	0.65	0.95	0.65	0.75
Maximum foliage biomass ($kg.tree^{-1}$)	30	17	40	20

2. CLIMATE CHANGE SCENARIOS

Six different well-established general circulation models (GCMs) included as part of the Intergovernmental Panel on Climate Change AR5 analysis (IPCC 2013; Table S6) were used to generate climate change scenarios. Two emissions pathways based on a representative CO_2 concentration pathways that generates radiative forcing of 4.5 Wm^{-2} (RCP 4.5) and 8.5 Wm^{-2} (RCP 8.5) (Meinshausen et al. 2011) were selected (Fig. S4).While the latter presents a high radiative forcing and greenhouses gases concentration, the former is an intermediate pathway that predicts stabilization in 2100-2150 and it is reflected in a large number of publications. GCMs were regional downscaled using the Statistical Downscaling Method (SDSM), a regression-based downscaling method that has been broadly applied to produce high-resolution climate change scenarios around the world (Wilby & Dawson 2013). Empirical relationships were established between data from weather stations for the period 1961-1990 and GCMs predictions interpolated into a 2.5º re-analysis grid NCEP/NCAR (Serrano et al. 2014). Maximum and minimum temperatures were predicted using unconditional models and minimum sum of absolute errors regression for parameter estimation: the variance of the series is increased by adding a random-residual factor to the deterministic component. Precipitation projections were made with conditional models by following the procedure specified by Kilsby et al. (1998) and the least square method. In this case, an additional stochastic process is included to determine whether a particular day precipitation occurred or not by comparing the probability obtained from the regression model and a pseudo-random number extracted from a uniform distribution with values between 0 and 1. Models were validated with observed data from the period 1991-2000 (Serrano et al. 2014). The projections from five near to study sites weather stations were averaged and subtracted or divided by temperature and precipitation, respectively, from climate series for the reference period 1975-2004 from each study site. The resulting data set spanned a 100-year period (2015–2114). Changes in growing season mean temperature and total precipitation are shown in Fig. S5.

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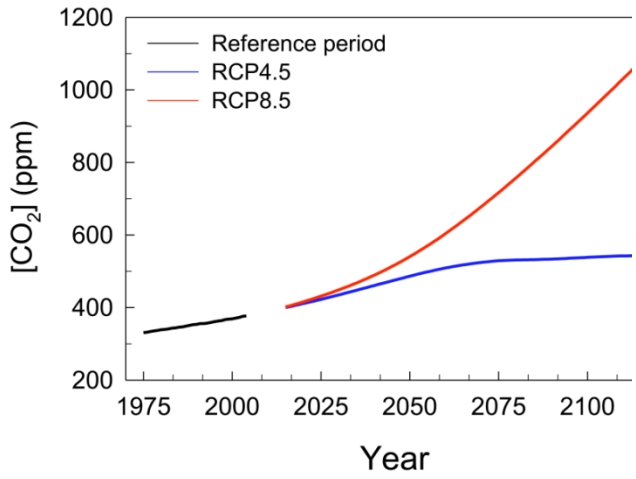

Figure S4. Atmospheric CO_2 concentration ($[CO_2]$) for the historical period 1975-2004 (black line) and projected increase for the RCP 4.5 (blue line) and RCP 8.5 emissions scenarios (red line).

Table S6. General Circulation Models (GCMs) used for climate change scenarios projections.

Name	Institution (Country)	References
BNU-ESM	Beijing Normal University (China)	Merrifield et al. (2013) , von Salzen et al. (2013)
CanESM2	Canadian Center for Climate Modelling and Analysis (Canada)	Arora et al. (2011), von Salzen et al. (2013)
CMCC-CM	Centro Euro-Mediterraneo per I Cambiamenti Climatici (Italy)	Fogli et al. (2009), Scoccimarro et al. (2011),
IPSL-CM5B-LR	Institut Pierre Simon Laplace (France)	Dufresne et al. (2012),
MIROC-ESM	University of Tokyo, National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology (Japan)	Watanabe et al. (2011)
MPI-ESM-MR	Max Planck Institute for Meteorology (Germany)	Stevens et al. (2012), Reick et al. (2013)

3. MIXTURES PERFORMANCE UNDER DIFFERENT CLIMATE SCENARIOS

Interaction effects at species level in Scots pine and European beech mixtures showed some temporal variability and differences among climate scenarios. Net complementarity interactions for both species were observed in the Mediterranean site, while in the continental site pine benefited in mixtures but beech presented net competitive interactions (Table S7).

Climate change predictions did not exert the same impacts on both species in mixtures at the two study sites. Climate impact on growth showed more positive tendency in the continental site. The projected warmer and dryer conditions promoted an important increase of species water stress, mainly in the Mediterranean site. This fact was translated in higher drought-related mortality rates, which reached peaks around 7 % and 16 % for pine and beech, respectively (Fig. S6).

Table S7. Mean (standard error) values of complementarity of stemwood biomass accumulation at species level for both study sites. Complementarity has been calculated following Eq.3. Three climate scenarios are presented: historical climate, moderate (RCP 4.5) and severe (RCP 8.5) climate change scenarios; see main text for further details. Bold values in climate change scenarios are statistically different from those simulated under reference climate.

		Mediterranean site (Aspurz)		**Continental site** (Garde)	
		P. sylvestris	***F. sylvatica***	***P. sylvestris***	***F. sylvatica***
Historical climate	50	19.32	-1.92	-9.27	-6.10
	75	49.04	6.72	9.96	-21.44
	100	63.39	59.74	15.87	-26.08
	125	75.42	88.18	18.71	-28.94
	150	81.14	77.05	19.69	-36.66
RCP 4.5 scenario	50	**14.26 (0.59)**	**-4.08 (0.48)**	**-11.81 (0.19)**	**-3.54 (0.52)**
	75	**42.99 (1.25)**	10.32 (3.61)	**8.24 (0.28)**	-22.07 (1.77)
	100	**65.51 (1.87)**	**30.19 (9.50)**	**16.56 (0.59)**	**-37.81 (1.98)**
	125	77.68 (3.41)	83.20 (19.02)	**21.31 (0.79)**	**-47.65 (2.00)**
	150	83.37 (2.99)	**146.66 (21.99)**	**24.10 (1.47)**	**-47.96 (2.13)**
RCP 8.5 scenario	50	**12.39 (0.99)**	**-4.99 (0.66)**	**-11.99 (0.39)**	**-3.15 (0.30)**
	75	**42.17 (0.79)**	**25.20 (7.43)**	**8.05 (0.60)**	**-20.59 (0.79)**
	100	**68.39 (4.77)**	**46.33 (11.15)**	**16.45 (0.48)**	**-33.88 (1.79)**
	125	**82.50 (3.92)**	108.28 (26.48)	**24.29 (1.40)**	**-40.14 (2.87)**
	150	80.62 (3.53)	**185.59 (36.16)**	**35.53 (2.94)**	**53.10 (25.95)**

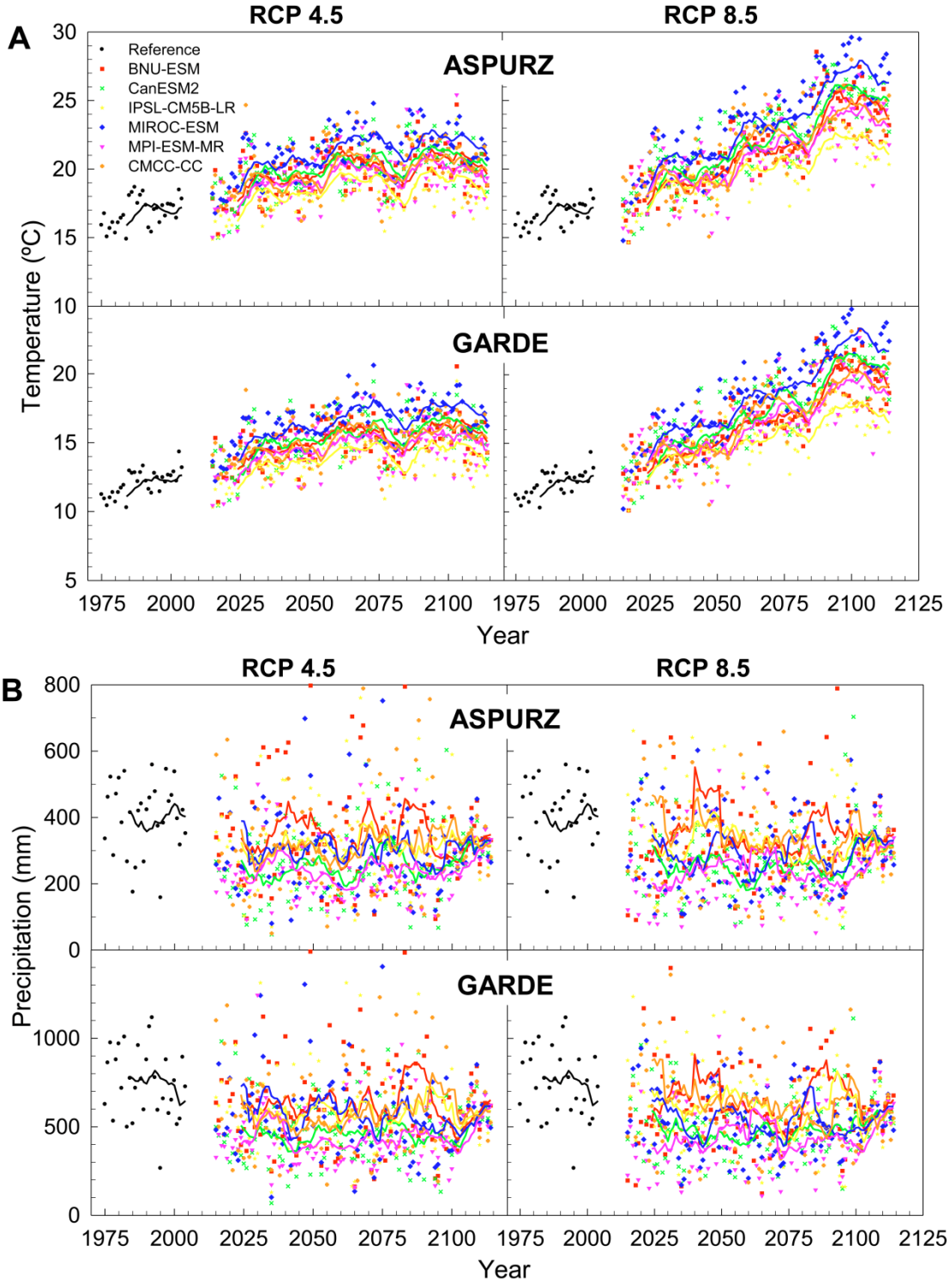

Figure S5. Study sites growing season (May-October) mean daily air temperature (A) and total precipitation (B) for the reference period 1975-2004 (in black) and projected for the next 100 years of two different emission scenarios: RCP 4.5 (left) and RCP 8.5 (right). Lines represent the 10-year moving average. Different colours represent different GCMs: BNU-ESM (red), CanESM2 (green), IPSL-CM5B-LR (yellow), MIROC-ESM (blue), MPI-ESM-MR (pink), and CMCC-CM (orange). Aspurz: Mediterranean, low-elevation site; Garde: continental, high-elevation site.

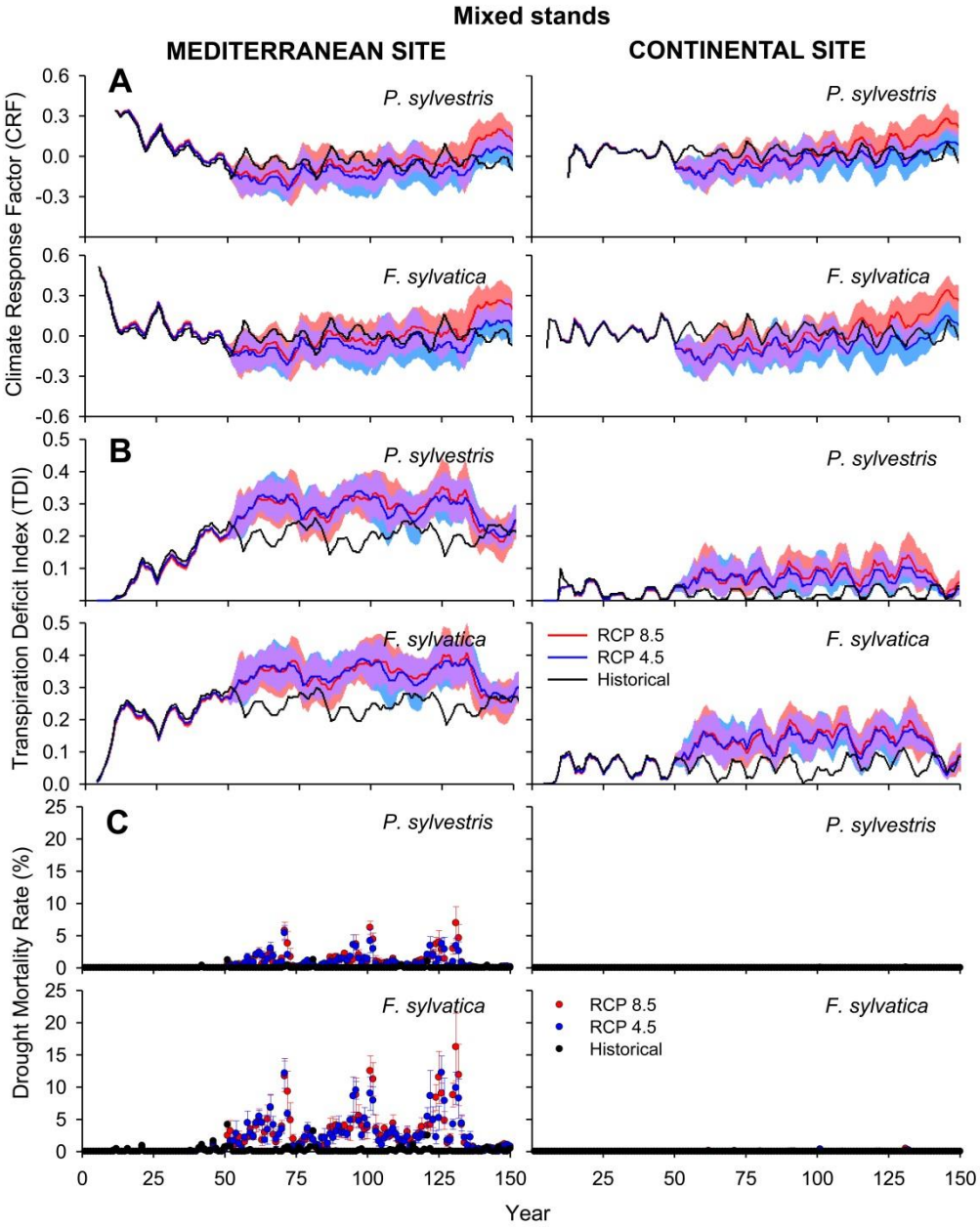

Figure S6. Climate impacts on species in Scots pine and European beech mixtures simulated with FORECAST Climate model. (A) Climate impact on species growth (Climate Response Factor; CRF) determined from Fig. S2A and B. (B) Water stress index (Transpiration Deficit Index; TDI) calculated as in Eq. 1. (C) Water stress-related mortality rate as a response of 2-year running average TDI derived from Fig. S3. Different colours indicate climate scenarios: historical (red), moderate (RCP 4.5; blue) and severe climate change (RCP 8.5; red). In (A) and (B) thick lines represent average and color areas represent 95% and 5% percentiles; the purple area indicates values that can be achieved by either moderate or severe climate change scenarios. In (C) error bars represent standard errors.

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